Fishery Bulletin

Vol. 79, No. 4 October 1981

McHUGH, J. L. Marine fisheries of Delaware 575
DURBIN, EDWARD G., and ANN G. DURBIN. Assimilation efficiency and nitrogen excretion of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae) 601
GRUBER, S. H., and L. J. V. COMPAGNO. Taxonomic status and biology of the bigeye thresher, *Alopias superciliosus* 617
PEARSON, WALTER H., PETER C. SUGARMAN, DANA L. WOODRUFF, and BORI L. OLLA. Impairment of the chemosensory antennular flicking response in the Dungeness crab, *Cancer magister*, by petroleum hydrocarbons 641
SHLOSSMAN, PHILIP A., and MARK E. CHITTENDEN, JR. Reproduction, movements, and population dynamics of the sand seatrout, *Cynoscion arenarius* . 649
IRVINE, A. BLAIR, MICHAEL D. SCOTT, RANDALL S. WELLS, and JOHN H. KAUFMAN. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida 671
STEVENSON, DAVID K., and FRANCISCO CARRANZA. Maximum yield estimates for the Pacific thread herring, *Opisthonema* spp., fishery in Costa Rica 689
KENDALL, ARTHUR W., JR., and N. A. NAPLIN. Diel-depth distribution of summer ichthyoplankton in the Middle Atlantic Bight 705
WEBB, P. W. Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivore, *Amphiprion percula* 727
FLINT, R. WARREN, and NANCY N. RABALAIS. Gulf of Mexico shrimp production: A food web hypothesis 737
GABRIEL, WENDY L., and WILLIAM G. PEARCY. Feeding selectivity of dover sole, *Microstomus pacificus*, off Oregon 749
TOLL, RONALD B., and STEVEN C. HESS. Cephalopods in the diet of the swordfish, *Xiphias gladius*, from the Florida Straits 765
HACUNDA, JOHN S. Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine 775

Notes

BOEHLERT, GEORGE W. The effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diploproa* and a comparison with growth in the field . 789

(Continued on back cover)

Seattle, Washington

U.S. DEPARTMENT OF COMMERCE
Malcolm Baldrige, *Secretary*

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
John V. Byrne, *Administrator*

NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

EDITOR

Dr. Carl J. Sindermann
Scientific Editor, *Fishery Bulletin*
Northeast Fisheries Center Sandy Hook Laboratory
National Marine Fisheries Service, NOAA
Highlands, NJ 07732

Editorial Committee

Dr. Bruce B. Collette
National Marine Fisheries Service

Dr. Edward D. Houde
Chesapeake Biological Laboratory

Dr. Merton C. Ingham
National Marine Fisheries Service

Dr. Reuben Lasker
National Marine Fisheries Service

Dr. Donald C. Malins
National Marine Fisheries Service

Dr. Jerome J. Pella
National Marine Fisheries Service

Dr. Jay C. Quast
National Marine Fisheries Service

Dr. Sally L. Richardson
Gulf Coast Research Laboratory

Kiyoshi G. Fukano, Managing Editor

The *Fishery Bulletin* (USPS 090-870) is published quarterly by Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Bin C15700, Seattle, WA 98115. Second class postage paid to Finance Department, USPS, Washington, DC 20260.

Although the contents have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget through 31 March 1982.

Fishery Bulletin

CONTENTS

Vol. 79, No. 4 October 1981

McHUGH, J. L. Marine fisheries of Delaware 575
DURBIN, EDWARD G., and ANN G. DURBIN. Assimilation efficiency and nitrogen excretion of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae) 601
GRUBER, S. H., and L. J. V. COMPAGNO. Taxonomic status and biology of the bigeye thresher, *Alopias superciliosus* 617
PEARSON, WALTER H., PETER C. SUGARMAN, DANA L. WOODRUFF, and BORI L. OLLA. Impairment of the chemosensory antennular flicking response in the Dungeness crab, *Cancer magister*, by petroleum hydrocarbons 641
SHLOSSMAN, PHILIP A., and MARK E. CHITTENDEN, JR. Reproduction, movements, and population dynamics of the sand seatrout, *Cynoscion arenarius* . 649
IRVINE, A. BLAIR, MICHAEL D. SCOTT, RANDALL S. WELLS, and JOHN H. KAUFMAN. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida 671
STEVENSON, DAVID K., and FRANCISCO CARRANZA. Maximum yield estimates for the Pacific thread herring, *Opisthonema* spp., fishery in Costa Rica 689
KENDALL, ARTHUR W., JR., and N. A. NAPLIN. Diel-depth distribution of summer ichthyoplankton in the Middle Atlantic Bight 705
WEBB, P. W. Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivore, *Amphiprion percula* 727
FLINT, R. WARREN, and NANCY N. RABALAIS. Gulf of Mexico shrimp production: A food web hypothesis 737
GABRIEL, WENDY L., and WILLIAM G. PEARCY. Feeding selectivity of dover sole, *Microstomus pacificus*, off Oregon 749
TOLL, RONALD B., and STEVEN C. HESS. Cephalopods in the diet of the swordfish, *Xiphias gladius*, from the Florida Straits 765
HACUNDA, JOHN S. Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine 775

Notes

BOEHLERT, GEORGE W. The effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diploproa* and a comparison with growth in the field . 789

(Continued on next page)

Seattle, Washington

1982

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402—Subscription price per year: $12.00 domestic and $15.00 foreign. Cost per single issue: $3.00 domestic and $3.75 foreign.

Contents–continued

LOVE, MILTON S., and WILLIAM V. WESTPHAL. A correlation between annual catches of Dungeness crab, *Cancer magister*, along the west coast of North America and mean annual sunspot number 794
ENNIS, G. P. Fecundity of the American lobster, *Homarus americanus*, in Newfoundland waters 796
AINLEY, DAVID G., ANTHONY R. DeGANGE, LINDA L. JONES, and RICHARD J. BEACH. Mortality of seabirds in high-seas salmon gill nets 800
O'CONNELL, CHARLES P., and PEDRO A. PALOMA. Histochemical indications of liver glycogen in samples of emaciated and robust larvae of the northern anchovy, *Engraulis mordax* 806

INDEX, VOLUME 79 813

Vol. 79, No. 3 was published 5 November 1981.

The National Marine Fisheries Service (NMFS) does not approve, recommend or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

MARINE FISHERIES OF DELAWARE[1,2]

J. L. McHUGH[3]

ABSTRACT

Delaware is almost in the geographical center of the Middle Atlantic Bight. The fisheries harvest endemic species, more or less restricted to the area, boreal species that migrate south in winter, and warmwater species that come north in summer. About 85 species have been recorded in commercial and recreational fisheries. Some have produced substantial catches, and the total commercial catch reached a peak in 1953 at nearly 167,000 metric tons. Production of commercial fisheries has since dropped to a low of only 305 metric tons in 1968, a drop of 99.8%, and has remained not much higher than that level ever since. Most of this decline was caused by the decline of the dominant menhaden fishery to zero in 1967, but drops in food finfishes and food shellfishes have been substantial also. The history has been one of boom or bust since the beginning, but superimposed upon this has been a gradual decline in almost all species. Several fisheries, notably purse seine, otter trawl, clam dredge, haul seine, and pound net, have ceased altogether.

The recreational fisheries have been growing in numbers of fishermen and in catches. Comparing food finfishes only, because industrial fisheries have no counterpart in the recreational fishery, and shellfishes have never been compared adequately, the recreational fisheries may now be taking three times as much as the commercial.

The boom and bust characteristic of the commercial fisheries has been caused by the widely fluctuating and uncertain nature of the major species, menhaden, blue crab, weakfish, croaker, and spot. Others, like surf clam, oyster, alewives, horseshoe crab, sturgeon, shad, and hard clam, have declined from overfishing, adverse changes in the inshore environment, or both. Some, like blue crab and weakfish, are fairly abundant at present, and weakfish is taken mostly by recreational fishermen. Others, like menhaden, have succumbed to heavy fishing of younger fish farther south. Menhaden vessels are now refrigerated, and can stay out longer and travel farther, which reduces the number of plants needed. Menhaden are still taken in Delaware Bay, but landed elsewhere.

The oceanographic regime is highly variable and not conducive to regular movements of northern or southern species into the area. These fisheries probably would be highly variable even if other changes had not also intervened. Maintaining them at fairly high levels will require cooperation from other states, cooperation which has not been forthcoming up to now. The State-Federal Fishery Management Board may help to improve interstate cooperation. The shellfisheries are more likely to survive, but to do so they will require enlightened management. The popular food fishes are likely to continue to decline as commercial species and become largely recreational. Some attention to the balance between commercial and recreational fisheries probably should be given soon.

The marine fisheries of the State of Delaware in many respects characterize the marine fisheries of the Middle Atlantic Bight region (New York to Virginia) as a whole. Delaware Bay is in the geographical center (lat. 39° N) of the section of coast from Cape Cod, Mass. (lat. 42° N), to Cape Hatteras, N.C. (lat. 36° N), and its marine fisheries have relied on three general classes of marine resource: 1) endemic species, more or less restricted to the region, or at least restricted in their migrations, such as surf clam, *Spisula solidissima*, and American oyster, *Crassostrea virginica*; 2) boreal species that migrate seasonally into the region in winter, such as Atlantic cod, *Gadus morhua*, or silver hake, *Merluccius bilinearis*; and 3) temperate water species that migrate north in summer, like Atlantic croaker, *Micropogonias undulatus*, or weakfish, *Cynoscion regalis*. Delaware is far enough south so that it does not usually get large quantities of boreal species, but it does on occasion have large numbers of southern species in the area.

June and Reintjes (1957), with respect to the fisheries of New Jersey, Delaware, and Maryland, noted that this area more or less marks the center of geographical distribution of migratory fish stocks which range between Cape Cod and Cape Hatteras. They pointed out that it is the southern

[1]The studies on which this paper is based were supported in part by grants from the New York Sea Grant Institute.
[2]Contribution No. 292 of the Marine Sciences Research Center of the State University of New York, Stony Brook, N.Y.
[3]Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794.

Manuscript accepted June 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

limit of such species as the Atlantic cod; haddock, *Melanogrammus aeglefinus*; American lobster, *Homarus americanus*; and others which come down from the north, and the northern edge of the range of black drum, *Pogonias cromis*; red drum, *Sciaenops ocellatus*; spot, *Leiostomus xanthurus*; and other southern species. They also noted that it is one of the most productive coastal regions in North America, which in 1953 produced over 662 million lb (300,300 t (metric tons)) of fishes and shellfishes, with an estimated value of $11.5 million to fishermen, and was capable of producing a great deal more. We could not reproduce these figures exactly from the 1953 statistics, but they were not far off. Total fishes were about 815 million lb (369,700 t), worth $12.7 million to fishermen, and the total commercial catch for the three States, including shellfishes, was about 891 million lb (404,200 t) worth about $31 million. By 1977 this had dropped to a commercial catch of 150 million lb (68,040 t) of fishes, 93 million lb (42,200 t) of shellfishes, for a total of only 243 million lb (110,200 t) worth about $70.5 million to fishermen. To this should be added 149 million lb (67,600 t) of fishes and 24.7 million lb (11,200 t) of shellfishes caught by recreational fishermen in 1974. These figures are not comparable with the recreational catch in 1953, which was presumably for the outer coast only, and did not include shellfishes. Nevertheless, it is fairly obvious that the recreational catch was larger in 1974. In 1947 dollars the two values were almost identical, $38.7 and $38.9 million. This is not consistent with the view that these fisheries were underexploited in 1953.

Reintjes and Roithmayer (1960) extended these studies for another 4 yr (1954-57 inclusive) and concluded that the region supports large populations of resident species and seasonal concentrations of migratory fishes. They concluded that production of fishes and shellfishes in the area appeared to be the highest per unit area in the Western Hemisphere, and that the fisheries generally were underexploited and underutilized. Using Rounsefell and Everhart's (1953) criteria, they found that of resident benthic species, such as summer flounder, *Paralichthys dentatus*; black sea bass, *Centropristis striata*; butterfish, *Peprilus triacanthus*; and scup, *Stenotomus chrysops*; only black sea bass appeared to be exploited at the maximum. Sedentary benthic species included surf clam and sea scallop, *Placopecten magellanicus*, and these and ocean quahog, *Arctica islandica*, and others were not overtaxed at that time. Migratory coastal species, like Atlantic menhaden, *Brevoortia tyrannus*; croaker; Atlantic cod; silver hake; weakfish; spot; red hake, *Urophycis chuss*; and bluefish, *Pomatomus saltatrix*, fluctuated widely and created greater instability in the fisheries than any other component of the total resource. Finally, migratory pelagic species like tuna, *Thunnus* sp.; sharks, Class Chondrichthyes; round herring, *Etrumeus teres*; sand lance, *Ammodytes* sp.; squids, *Loligo* sp. and *Illex* sp.; and others, were all abundant but in 1957 unexploited.

Pt imutter (1959) on the other hand, considering the fisheries of a wider area, from New York to Virginia inclusive, concluded that of the five major species other than menhaden and alewives—namely croaker, weakfish, scup, summer flounder, and black sea bass—only black sea bass appeared not to have declined in abundance. Thus, the picture is not entirely clear, and previous authors have not agreed. It must be pointed out, however, that those authors were not looking at precisely the same set of fisheries.

Eight fish and shellfish species have produced commercial landings >1,000 t (2,204,000 lb) in Delaware at some time in the recorded history of commercial fisheries in the State (Table 1). Another 10 species have at one time or another yielded commercial landings between about 1,000 and 100 t (2.2 million and 220,000 lb). Altogether, in recorded history from 1880 to 1978 inclusive (Pileggi and Thompson 1978), about 85 aquatic species or groups of species have been recorded in commercial or recreational marine fishery landings in Delaware. All species or groups of species are listed in Tables 1 and 2. Major species are discussed later in descending order of maximum annual landed weight.

The commercial fisheries of Delaware have been substantial in their time, peaking at nearly 167,000 t (370 million lb) in 1953 (Figure 1), but falling off after 1962 to a low of only 305 t (673,000 lb) by 1968. This was once the fourth largest State along the Atlantic coast in total landings. By far the most important species in terms of weight was menhaden, which reached a peak of 164,000 t (>360 million lb) in 1953 (Figure 2). Setting aside menhaden, which in most years made up the bulk of the catch, and the horseshoe crab, *Limulus polyphemus*, total food finfishes emerge as declining steadily since landings were first recorded (Figure 3), beginning in 1887 with a total of nearly

TABLE 1.—Maximum domestic commercial landings by species in the State of Delaware since 1880 and year of maximum landings. Species arranged in decreasing order of maximum landings. Weights in metric tons.

Species	Maximum landings and year	Secondary peak and year	Species	Maximum landings and year	Secondary peak and year
Atlantic menhaden, *Brevoortia tyrannus*	163,679 (1953)		American lobster, *Homarus americanus*	15 (1887, 1888)	14 (1971)
Surf clam, *Spisula solidissima*	3,962 (1970)		Suckers, family Catostomidae	16 (1897)	
Blue crab, *Callinectes sapidus*	2,233 (1957)		Northern kingfish, *Menticirrhus saxatilis*	15 (1956)	
American oyster, *Crassostrea virginica*	1,969 (1954)		Atlantic mackerel, *Scomber scombrus*	14 (1967)	
Weakfish, *Cynoscion regalis*	1,457 (1889)		Terrapin, *Malaclemys* sp.	14 (1880)	
Alewife, *Alosa pseudoharengus*, *A. aestivalis*	1,449 (1930)		Red crab, *Geryon quinquedens*	12 (1977)	
Horseshoe crab, *Limulus polyphemus*	1,352 (1908)	907 (1976)	Mussel, *Mytilus edulis*	10 (1932)	
Atlantic sturgeon, *Acipenser oxyrhynchus*	1,281 (1887)		Squids, *Loligo opalescens*, *Illex illecebrosus*	10 (1952)	
American shad, *Alosa sapidissima*	735 (1897)		Atlantic herring, *Clupea harengus*	9 (1948)	
Atlantic croaker, *Micropogonias undulatus*	510 (1930)	303 (1955)	King mackerel, *Scomberomorus cavalla*	8 (1951)	
Hard clam, *Mercenaria mercenaria*	414 (1951)		Unclassified flounders	5 (1977)	
Spot, *Leiostomus xanthurus*	294 (1880)	103 (1955)	American plaice, *Hippoglossoides platessoides*	4 (1947)	
Striped bass, *Morone saxatilis*	266 (1973)		Northern puffer, *Sphoeroides maculatus*	3 (1963)	
Mullet, *Mugil cephalus*	264 (1931)		Unclassified sharks	3 (1955)	
American eel, *Anguilla rostrata*	198 (1887)		Sheepshead, *Archosargus probatocephalus*	3 (1880)	
Conchs, *Busycon* spp.	189 (1976)		Minnows, family Cyprinidae	2 (1957)	
White perch, *Morone americana*	181 (1897)		Silver perch, *Bairdiella chrysoura*	2 (1939)	
Common carp, *Cyprinus carpio*	98 (1904)		Grayfish, *Squalus acanthias*, *Mustelus canis*	2 (1975)	
Summer flounder, *Paralichthys dentatus*	95 (1958)		Red drum, *Sciaenops ocellatus*	1 (1926)	
Red hake, *Urophycis chuss*	92 (1947)		Yellowtail flounder, *Limanda ferruginea*	1 (1930)	
Silver hake, *Merluccius bilinearis*	92 (1947)		Hickory shad, *Alosa mediocris*	1 (1948)	
Black sea bass, *Centropristis striata*	82 (1975)		Black bass, *Micropterus* spp.	1 (1908)	
Scup, *Stenotomus chrysops*	71 (1949)		Gizzard shad, *Dorosoma cepedianum*	1 (1932)	
Catfish and bullheads, family Ictaluridae	68 (1908)		Frogs, *Rana* spp.	1 (1908, 1926)	
Yellow perch, *Perca flavescens*	68 (1880)	22 (1930)	Unclassified food fishes	[1] (1977)	
Black drum, *Pogonias cromis*	62 (1880)	14 (1956)	White hake, *Urophycis tenuis*	[1] (1976)	
Snapper turtle, *Chelydra serpentina*, *Macrochelys temminckii*	60 (1955)		Shrimp, *Palaemonetes vulgaris* or *Crangon septemspinosus*	[1] (1887, 1888)	
Atlantic cod, *Gadus morhua*	59 (1944)		Soft clam, *Mya arenaria*	[1] (1887, 1888)	
Tautog, *Tautoga onitis*	34 (1930)		Sunfish, family Centrarchidae	[1] (1901)	
Bluefish, *Pomatomus saltatrix*	32 (1931)	29 (1949)	Atlantic bonito, *Sarda sarda*	[1] (1935, 1953)	
Butterfish, *Peprilus triacanthus*	31 (1949)		Conger eel, *Conger oceanicus*	[1] (1935)	
Unclassified industrial fishes	27 (1958)				
Winter flounder, *Pseudopleuronectes americanus*	23 (1966)				
Jonah crab, *Cancer borealis*	20 (1977)				
Pike or pickerel, *Esox* spp.	19 (1897)				

[1] One-half t or less.

TABLE 2.—Species reported as caught by recreational fishermen in Delaware waters and not included in Table 1.

Species	Species	Species	Species
Skates, family Rajidae	Dolphin, *Coryphaena* sp.	Yellowfin tuna, *T. albacares*	Wahoo, *Acanthocybium solanderi*
Stingray, *Dasyatis* sp.	Pigfish, *Orthopristis chrysoptera*	Albacore, *T. alalunga*	White marlin, *Tetrapturus albidus*
Lizardfish, *Synodus* sp.	Tunas, *Thunnus* spp.	Little tunny, *Euthynnus alletteratus*	Searobins, *Prionotus* spp.
Oyster toadfish, *Opsanus tau*	Bluefin tuna, *T. thynnus*	Spanish mackerel, *Scomberomorus maculatus*	Spiny boxfish?, *Lactophrys* sp.?
Goosefish, *Lophius americanus*	Blackfin tuna, *T. atlanticus*		
Amberjack, *Seriola* sp.			

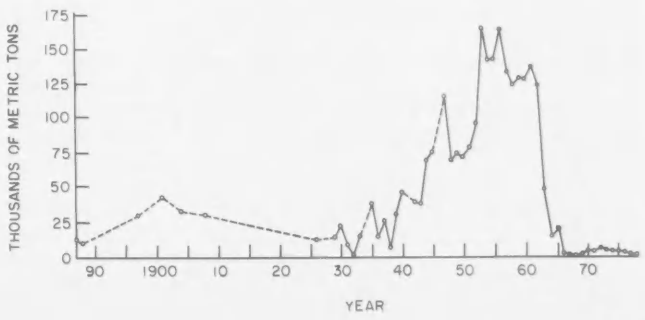

FIGURE 1.—Total commercial landings, all species, in Delaware, 1887-1978. When years were missing, points were joined by broken lines.

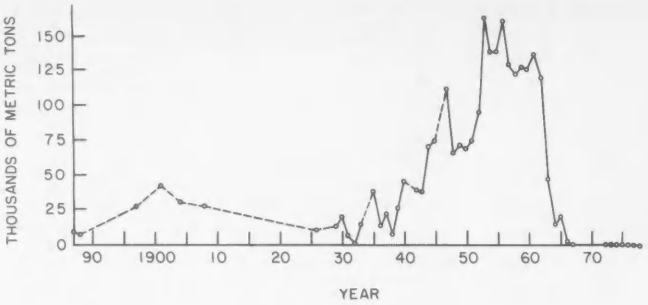

FIGURE 2.—Total landings of industrial fishes and shellfishes in Delaware, 1887-1978.

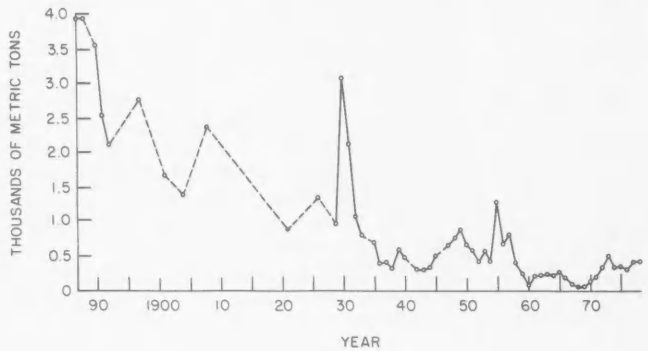

FIGURE 3.—Total commercial landings of food finfishes in Delaware, 1887-1978.

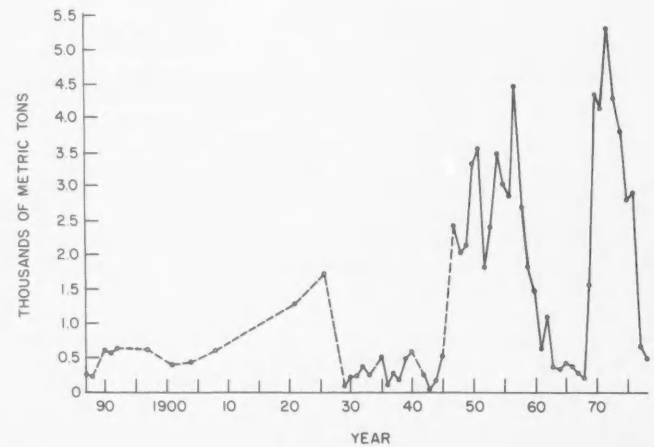

FIGURE 4.—Total commercial landings of food shellfishes in Delaware, 1887-1978.

4,000 t (9 million lb), falling by 1969 to a low of 65 t (143,000 lb), then rising to 418 t (921,000 lb) by 1977. This was a decline from peak to valley of about 98.4%. Species that contributed mainly to this drop were Atlantic sturgeon, *Acipenser oxyrhynchus*; American shad, *Alosa sapidissima*; alewife, *A. pseudoharengus* and *A. aestivalis*; and white perch, *Morone americana*, all anadromous species. Later croaker, weakfish, spot, and striped bass, *Morone saxatilis*, also dropped substantially, all species with a close coastal or anadromous life history. The drop was not all caused by a reduction in abundance of these species, since effort in most fisheries was dropping too.

The shellfishes had quite a different history (Figure 4), peaking in 1926 at about 1,800 t (nearly 4 million lb), in 1957 at 4,500 t (nearly 10 million lb), and in 1972 at 5,400 t (nearly 12 million lb). This was interspersed with lows of <54 t (120,000 lb) in 1943, 232 t (512,000 lb) in 1968, and 685 t (1,511,000 lb) in 1977, drops of 94.3, 94.8, and 87.2%, respectively. These represent three periods in the history of the shellfisheries of Delaware, oyster peaking in 1926, blue crab, *Callinectes sapidus*, in 1957, and surf clam rising briefly in the early 1970's.

The history of Delaware's commercial fisheries has been one of boom and bust since the beginning. The causes have been the wide fluctuations in availability, referred to already, associated with species at the limits of their geographic ranges, plus overexploitation and degraded habitat. The menhaden industry harvested its last fish with purse seines in 1966, the food finfish industry has declined fairly steadily, and the shellfish industry has had at least three major ups and downs in the last 50 yr. Several fisheries have ceased completely. What are the prospects for the future of Delaware's fisheries?

INDUSTRIAL FISHERIES

Industrial fisheries have consisted mostly of menhaden, with lesser amounts of horseshoe crab from time to time. The industrial fisheries were relatively small until 1944, when they rose above 100 million lb for the first time. They remained fairly large until 1963, and quickly collapsed after that. The last purse seine catch landed in Delaware was in 1966. Menhaden are still caught in Delaware waters but are landed elsewhere. Prior to the mid-1940's the fishery was not well developed, probably because the Pacific sardine, *Sardinops sagax*, industry on the west coast was more efficient and was able to supply most of the markets. After 1945, the decline of the Pacific sardine industry and the growth of the broiler industry in the east opened up new markets, and the menhaden industry on the east coast prospered, especially after 1952. By 1963, declining recruitment, probably associated with heavy fishing farther south, affected the supply of fish to northern waters, and the last plant in Delaware closed at the end of the 1966 season.

A small reduction plant operated on horseshoe crab for a few years from 1930 to 1944. A small number was taken after 1966, probably for bait. The greatest landings recorded were about 500,000 lb in 1935. The decrease was largely caused by a reduction in demand, although horseshoe crab now may be less abundant than before (Daiber[4]). This conclusion, however, is largely intuitive.

FOOD FINFISHES

Landings of food finfishes in Delaware have been declining since the first record in 1887. There have been temporary increases, such as in 1930-31 and 1955, but for the most part it has been steadily downward (Figure 3). The anadromous species were the first to be affected. Sturgeon was first, dropping from a high of nearly 1,300 t (3 million lb) in 1887 to only 15 t (34,000 lb) by 1908. This was reflected also in the price, which was less than a cent a pound, on the average, in 1887, but had risen to over 20¢/lb by 1908. Shad was not far behind, dropping from about 800 t (1.4 million lb) in 1890 to 18 t (39,000 lb) in 1931, while the price rose from <4¢ to about 18¢/lb. Alewife catches reached their peak later, at about 1,450 t (3.2 million lb) in 1930. By 1938 they had dropped to 21 t (47,000 lb), and never exceeded 60 t (150,000 lb) after that. White perch, another anadromous species, produced the greatest landings in 1897 at about 180 t (297,000 lb), and by 1940 was down to 7 t (16,000 lb).

Coastal fishes were equally temporary. Weakfish was the most important species, with total landings of about 1,500 t in 1889 (3,212,000 lb), later fluctuating several times, and finally dropping to a low of only 2 t (5,000 lb) in 1968.

[4]Franklin C. Daiber, Professor of Marine Biology and Biological Sciences, College of Marine Studies, University of Delaware, Newark, DE 19711, pers. commun. December 1979.

Croaker produced 500 t (>1 million lb) in 1930 and was down to nothing in 1961 for over a decade. Spot produced almost 300 t (649,000 lb) in 1880 and was highly variable after that, dropping to nothing in 1961 for over a decade, then showing up again in 1975. Spot is salted down for personal use by local fishermen, and some parts of the catch are not reported. Striped bass was never a large commercial producer in Delaware, and in fact reached its peak in 1973 at about 265 t (586,000 lb).

FOOD SHELLFISHES

Landings of shellfishes, minus seed oysters, which appear later as market oysters, and horseshoe crabs, which are used to make meal or as bait, have an interesting history. The principal species are only four: American oyster, blue crab, surf clam, and hard clam, *Mercenaria mercenaria*. The total take of these species has been highly variable, fluctuating from almost nothing to nearly 5,500 t (12 million lb), with different species making up most of the landings at each peak. Almost the entire peak in 1926 was made up of American oyster (Figure 4), 1,554 t (3,426,000 lb). In 1951 and 1957 the major species was blue crab, with American oyster second. Blue crab landings peaked in 1951 and 1957 at 2,260 t (nearly 5 million lb). The peak in 1972 was caused mostly by landings of 3,879 t (8,551,000 lb) of surf clam.

American oyster was relatively high in the early days, dropped to a low of only 22 t (48,000 lb) in 1943, peaked again from 1947 to 1958 with a maximum of 1,968 t (4,340,000 lb) in 1954, reached an all-time low of 15 t (33,000 lb) in 1961, and since has come back partially, reaching a high of 230 t (509,000 lb) in 1972. Blue crab dropped to a low in 1968, and since have risen to 1,655 t (3,650,000 lb) in 1976. Surf clam did not appear in landings until 1956, rose to a peak of 773 t (1,705,000 lb) in 1959, dropped to nothing in 1963, showed up again in 1969, peaked in 1970 at 3,962 t (8,734,000 lb), and dropped again to nothing in 1976. Hard clam built up to a peak of 414 t (912,000 lb) in 1951 and dropped to a low of 15 t (34,000 lb) in 1975. The only one of the four that appears to be reasonably healthy at the present time is the blue crab, but judging from past fluctuations blue crab can not be depended upon to maintain a healthy fishery, even if adequate management measures were in effect. Blue crab is near the northern limit of its range in Delaware, and probably can be expected to fluctuate widely for that reason.

RECREATIONAL FISHERIES

The recreational fisheries of Delaware, like marine recreational fisheries almost everywhere, are not well known. It can safely be assumed that they are growing, if the national surveys are a criterion, for catches have risen from 80,741 t (178 million lb) of food finfishes in 1960 to 121,564 t (about 268 million lb) in 1974. The rate of rise may have been greater than this, for in 1965 the estimated catch dropped to 58,060 t (128 million lb). These catches, however, are for the area from New York to Cape Hatteras, except for 1974, which did not include any part of the North Carolina coast. Only in 1974 was an estimate made of the Delaware catch, at about 2,903 t (6.4 million lb) of food finfishes, plus 1,814 t (about 4.0 million lb) of shellfishes. This consisted of 1,723 t (about 3.8 million lb) of weakfish, 227 t (about 500,000 lb) of bluefish, 84 t (185,000 lb) of sharks, 69 t (153,000 lb) of summer flounder, 227 t (500,000 lb) of other fishes; 998 t (2.2 million lb) of hard clam, 816 t (1.8 million lb) of soft clam, *Mya arenaria*, and a small amount of other shellfishes. If these figures are at all realistic, the food finfish catch of recreational fishermen in Delaware is substantially higher than the commercial catch.

This is confirmed by figures contained in sportfishing surveys conducted in 1953, 1954, and 1955. Using average weights of fishes from the 1970 saltwater angling survey (Deuel 1973), it was estimated that recreational fishermen caught 1,814 t (nearly 4 million lb) of fishes in 1955, which compared with 1,225 t (about 2.7 million lb) of the same species in the commercial catch. Estimates of recreational catches covered a period of only about 3 mo, whereas the commercial catch covered the entire year. Consequently, it is probably a conservative estimate that recreational fishermen took at least twice as much as commercial fishermen.

Later estimates made the discrepancy even greater, and this is not surprising, for the numbers of anglers were increasing also (Deuel 1973). Miller (1978) estimated that the recreational catch in 1977 was about 5.8 million fishes, plus considerable quantities of blue crab and hard clam. By weight, this would be perhaps 3,402 t (7.5 million lb), which was three times as great as the

commercial catch, and possibly more. This report also gave estimated landings by recreational fishermen for other years, 2.4 million fishes in 1968 and 1.9 million in 1973. Using the same average annual weights these amounted to roughly 1,542 t (3.4 million lb) and 1,225 t (2.7 million lb), respectively. This was 21 times and 2.3 times the commercial catch of finfishes, respectively. These are probably not very accurate, but it is clear that sportfishermen in Delaware caught more fishes than commerical fishermen.

THE OCEANOGRAPHIC REGIME

Parr (1933) found that through alternate development and breakdown of temperature barriers at Cape Cod-Nantucket Shoals and Cape Hatteras, the shallow water belt along the Middle Atlantic coast is in open-temperature continuity with the waters north of Cape Cod in winter and with waters south of Cape Hatteras in summer, being barred in opposite directions during these seasons. Temperatures in the Cape Cod region develop slowly in winter, early spring, and late fall, but show violent fluctuations in summer. In the Cape Hatteras region the opposite succession of conditions prevails, with relatively smooth temperature changes in summer, but with violent fluctuations in winter, early spring, and late fall. Winter invasions of fishes from the north are quantitatively poor and not very penetrating, but visitors from south of Cape Hatteras are usually complete. In the Delaware Bay region these changes are at a maximum, and Delaware Bay has the greatest difference between maximum and minimum temperature whether at the 5 percentile (Figure 5) or the 95 percentile (Figure 6) level. This means that the temperature regime is less variable to the north and south of Delaware, and presumably the effect on migrations is less. The data from which Figures 5 and 6 were taken are from Waters (1967). This shows for a period of over 100 yr the 5 percentile and 95 percentile isotherms of surface water temperatures along the Atlantic coast of North America. The temperature rises rapidly in spring and falls almost as rapidly in fall, and also varies considerably from time to time. For example, the 70° F isotherm penetrates only to Virginia in cool years (Figure 5), but rises as far north as Cape Cod in warm years (Figure 6) in summer. Similarly, in winter the 42° F isotherm comes as far south as Cape Hatteras in cold years, whereas in warm years it barely reaches Cape Cod.

This means that Delaware is in a region of rather highly variable water temperature, which will influence how far north southern species will come in summer, and how far south boreal species will come in winter. This is obviously not a favorable oceanographic regime for highly predictable fisheries, even if their numbers did not fluctuate greatly from time to time.

FISHES AND SHELLFISHES

Menhaden

Although it undoubtedly was abundant in the Delaware area, menhaden did not support a major commercial fishery in the early days. Along many parts of the coast it was originally used mainly as fertilizer, applied directly to agricultural land.

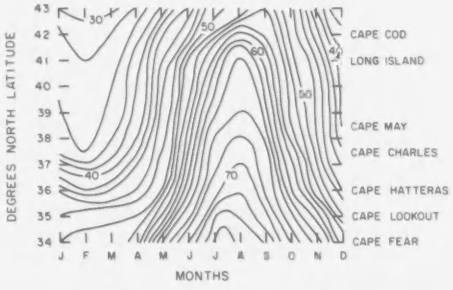

FIGURE 5.—Surface temperatures along the Middle Atlantic coast, 5 percentiles, by months and degrees latitude.

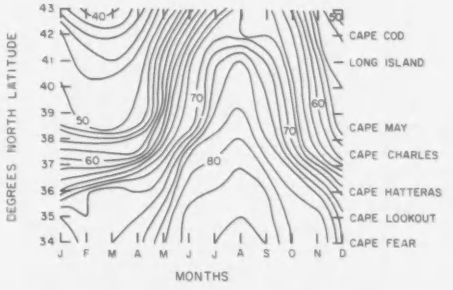

FIGURE 6.—Surface temperatures along the Middle Atlantic coast, 95 percentiles, by months and degrees latitude.

Most, if not all, of this harvest probably was not recorded in commercial landings. In 1880 (Collins 1887), 10 t (23,000 lb) of the total reported catch of 237 t (522,999 lb) landed in Delaware were used as human food. Modern usage of the resource is as raw material for production of oil, meal, and soluble proteins. Menhaden now is used only indirectly as a commercial food product, by incorporating meal and solubles in diets for poultry and livestock. The oil is used in a variety of products from paint to cosmetics.

By 1887 and 1888 a menhaden industry had developed in Delaware. Two factories were in operation at Lewes, employing 88 men ashore. Fishing vessels were powered by steam; 5 vessels and 107 fishermen operated in 1887, 4 vessels and 84 fishermen in 1888. Most of the catch at that time was made in gill nets but haul seines took about 27% of the total catch. The catch produced 878,206 l (232,000 gal) of oil and 3,000 tons of scrap (fish meal) in 1887; 582,455 l (153,870 gal) and 1,800 tons in 1888.

The method of recording landings and industrial production of menhaden used in the 1880's produced some inconsistent figures. It is obvious that landings of 100 t (220,399 lb) reported for Delaware in 1887 could not produce 878,206 l (232,300 gal) of oil and 3,000 tons of scrap. The discrepancy was caused by the method of allocating raw materials and processed products. The fishing vessels were registered in Connecticut and their catch was reported in their State of origin. The plants at Lewes, Del., were also built and owned by Connecticut interests, but their production was credited to Delaware, the State in which they were located.

Menhaden landings in Delaware can be estimated by using figures on menhaden production for the State. These are given, for the most part, in numbers of fish rather than in weight, a peculiar method of accounting for the greatest weight of fish landed, especially as we know that they were not counted. Menhaden were weighed by filling a bucket which held half a ton. In 1901 weight was given in numbers of fish, but it was also said that 1.67 fish weighed 1 lb, which was equivalent to 3,000 fish/ton. This conversion factor was used to calculate weight of fish in 1904 and earlier. In 1908 and thereafter, total landings for Delaware were given in pounds.

This peculiar way of handling menhaden could be quite misleading. For example, in Chesapeake Bay, the average weight of menhaden in the purse seine catch was about 3 or 4 fish to the pound, and probably is more now. In North Carolina it must be even greater. These are averages, and they will vary considerably from spring to fall, and with relative numbers of the different ages of fish. Thus, it is much more logical to quote menhaden landings by weight, since that is the way they are measured. A menhaden catch in Chesapeake Bay will contain considerably greater numbers of fish than one of the same weight in Delaware or farther north.

Menhaden landings in Delaware were fairly large in the early 1900's but fell to a low point in 1932 (Figure 7). This low point was partly caused by the depression, which reduced demand and prices, but also by the great overproduction of whale oil in 1931, which saturated world markets. The Pacific sardine fishery was also beginning about 1915, and the menhaden fishery did not develop fully until the late 1940's, when the Pacific sardine fishery began to collapse. The rise of the broiler industry, especially in the Delmarva Peninsula, also created favorable market condi-

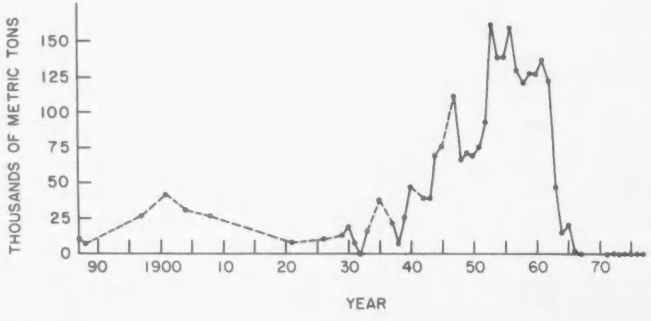

FIGURE 7.—Commercial landings of Atlantic menhaden in Delaware, 1887-1977.

tions. Catches were at a peak from 1953 to 1962, averaging 136,828 t (301,649,000 lb), after which they sharply declined, and the purse seine fishery, which was the dominant gear used until then, ended after the 1966 season. During this period Delaware was the most important State along the Atlantic coast in 1952 in menhaden landings, second in importance from 1953 to 1958, and second again in 1960 and 1961.

Surf Clam

Next to menhaden, surf clam produced the greatest weight of landings in Delaware, 3,962 t (8.7 million lb) in 1970. This was weight of meats only, equivalent to 28,123 t (about 62 million lb), live weight. This was not only the most recent fishery in Delaware, having produced the first small catch in 1956 (Figure 8), but also was relatively short lived. The fishery developed quickly but dropped to nothing by 1963, redeveloped in 1969, and produced its last catch in 1975. Figures on landings, however, do not tell the whole story. According to Daiber (footnote 4), a processing plant has been situated at Lewes for approximately 20 yr. At first, dredge boats landed directly at the plant, then as they fished farther away they landed the catch at other ports and surf clams were trucked to Lewes. More recently, vessels became larger, and when they worked near the mouth of Delaware Bay they landed at the docks of the former menhaden plants and surf clams were trucked the short distance to the processing plant. The vessels are now landing in New Jersey, and surf clams are trucked in, for the plant is still operating.

The fishery in the vicinity of Delaware was merely a phase of the fishery as a whole, which began off Long Island, N.Y., during the Second World War, and gradually shifted down the coast as ground after ground was overexploited. The peak was reached in 1974, off Virginia, and catches declined substantially after that. The Mid-Atlantic Council is now trying to manage the resource, along with ocean quahog.

Blue Crab

A small fishery for blue crab has existed in Delaware waters since the early days. Landings were not very large until after the Second World War, then shot up to 2,000 t (>4 million lb) in 1950 and 1951 (Figure 9). They dropped sharply in 1952, then rose gradually to nearly 2,265 t (5 million lb) in 1957, then dropped off to about 90 t (200,000 lb) by 1968. Subsequently, they have risen again and in 1975 and 1976 were 1,590 t (>3.5 million lb). The decline in 1977 probably was caused by an extremely cold winter.

Blue crab is abundant north to Chesapeake Bay, where it supports a major fishery. From Delaware north it appears spasmodically, sometime existing in great abundance, sometimes almost disappearing. It extends north to Cape Cod, and occasionally appears in the Gulf of Maine. The great variations in availability from Delaware Bay north are probably explained on the basis of environmental fluctuations, the major element of which is probably winter temperature. This is characteristic of a species near the northern limits of its range.

During the 1960's, however, it has been suggested that the intensive use of DDT in control of

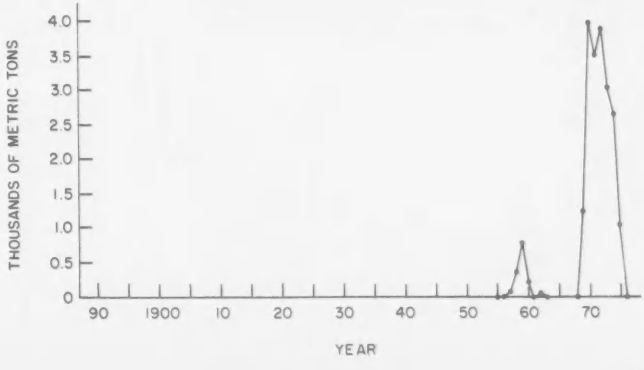

FIGURE 8.—Commercial landings of surf clam in Delaware, 1956-1975.

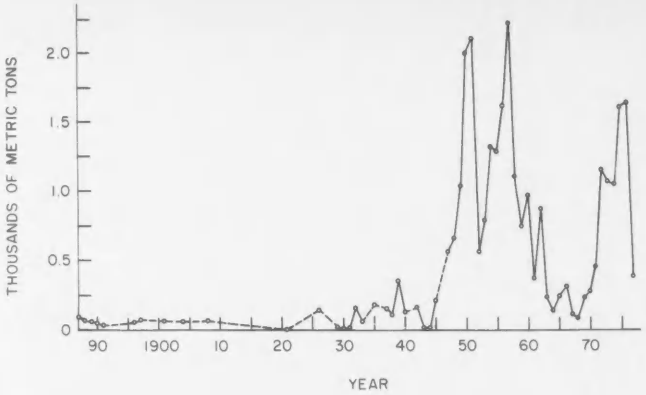

FIGURE 9.—Commercial landings of blue crab in Delaware, 1887-1977.

mosquitoes on coastal marshlands may have been a factor. It is suggestive in that blue crab has returned in great abundance to Delaware, New Jersey, New York, and even farther north. On the other hand, its abundance is obviously affected adversely by cold winters, such as the winter of 1976-77, which killed many of the blue crabs in New York waters. It is expected that blue crab will continue to be highly variable in abundance from Delaware north. At present, however, it is the most important fishery in the area.

Blue crab is an important predator of hard clam wherever it is abundant. In areas where extensive hard clam fisheries exist, or where the potential for hard clam production is high, it might be well to encourage fisheries for blue crab, and to place no limits on the catch, because there is an established and valuable fishery for hard clam, and the two may not be able to coexist in abundance.

American Oyster

The American oyster industry in Delaware was rather small for most of its history, taking most of its harvest from naturally producing grounds in the State. Prior to 1929 its history is not clear because landings were available for only 14 of the 49 yr. It appears that it peaked somewhere between 1912 and 1926 (Figure 10), then dropped off to low levels until after the Second World War. For about 12 yr, from 1947 to 1958, it fluctuated from about 900 to 1,800 t (2 to 4 million lb), then dropped abruptly, and since then has been <225 t (500,000 lb) except for 1 yr. Poor management, followed by disease, were the principal causes, according to Daiber (footnote 4).

Price (1978) has noted that in the late 1800's, Delaware Bay as a whole (New Jersey and Delaware) produced about 10,423 t (23 million lb)

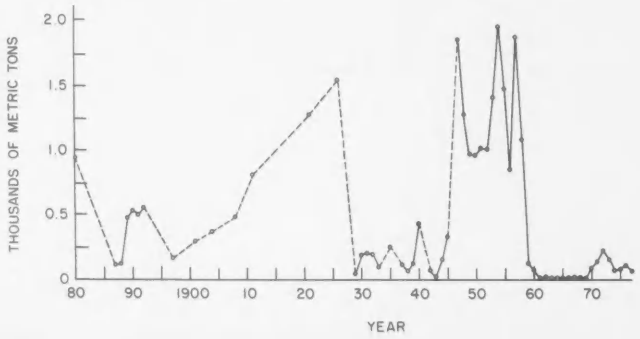

FIGURE 10.—Commercial landings of American oyster in Delaware, 1880-1977.

of American oysters, and had substantial shad, sturgeon, and other fisheries. A variety of factors, including improper management of shellfish beds (harvesting without replenishing equal quantities of shell stock), development of the watershed with attendant siltation, heavy industrialization of the Delaware River, industrial effluents and oil spills, mosquito control by ditching wetlands and spraying, and closure of harvesting areas caused by sewage contamination, caused American oyster production to decline to 4,082 t (9 million lb) by 1954. By 1960 the American oyster industry suffered a catastrophic collapse caused by the pathogen MSX (*Minchinia nelsoni*). In Delaware, the value of American oyster landings declined from almost $3 million to <$40,000 from 1954 to 1961. The fishery has not been reestablished to date (Maurer et al. 1971).

Gunter (1975) claimed that American oyster production in Delaware Bay as a whole (Delaware and New Jersey) has declined in two vast steps, from about 6,500 t (14,247,000 lb) from 1880 to 1931, to 3,600 t (7,951,000 lb) from 1932 to 1957, to 390 t (859,000 lb) from 1959 to 1970. He pointed out that the two declines each occurred 3 yr after diversions of Delaware River water to New York City in 1929 and 1953. He did not offer other data to substantiate cause and effect.

Weakfish

There is little question that weakfish was the "money" fish of the Delaware fishery. It has fluctuated widely in abundance from time to time, but has held up well, and may now be as abundant or more so, than it ever was. Although the record of commercial landings from 1880 to 1977 is in general downward (Figure 11), this is a popular sport fish, and recreational catches in recent years, if they are at all accurate, suggest that the catch remains at over 1,360 t (3 million lb). The resource obviously fluctuates widely in abundance for environmental reasons, of which more will be said later. It was relatively abundant in the 1950's and very low in abundance in the 1960's. The decline of the commercial fishery was probably a combination of these natural fluctuations and an increasing catch by the recreational fishery. The estimated catch by sport fishermen in 1974 was 1,724 t (about 3.8 million lb). Assuming a much smaller recreational catch in the 1880's, this compares favorably or even exceeds earlier catches. Some also have suggested that the decline in abundance of weakfish after the Second World War may have been caused by widespread use of DDT on salt marshes (Joseph 1972).

The gradual decline in the take of weakfish by commercial fishermen probably contributed to the virtual collapse of the commercial fisheries generally in Delaware. Sturgeon, shad, and croaker, the other major contributors to the inshore fishery, had already been reduced in abundance much earlier, and with weakfish virtually gone, there was little else to attract commercial fishermen. This probably was hastened by recreational fishermen, who discovered an old law some time in the 1960's that prohibited trawling in Delaware Bay and applied pressure to have it observed. New Jersey fishermen have not been allowed to trawl in the Bay for many years.

Alewives

Except for a brief period in the early 1930's, alewives were a relatively small and declining resource in Delaware (Figure 12). Catches declined fairly steadily, until by the 1960's they were almost zero. The brief increase in alewife landings in the early 1930's may have been caused by the

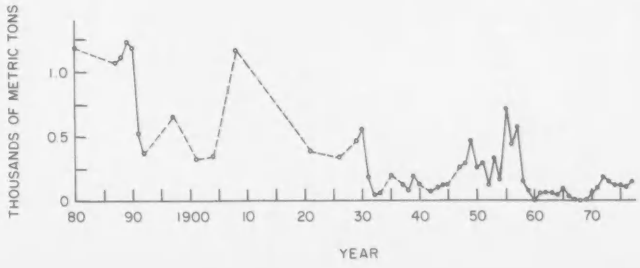

FIGURE 11.—Commercial landings of weakfish in Delaware, 1880-1977.

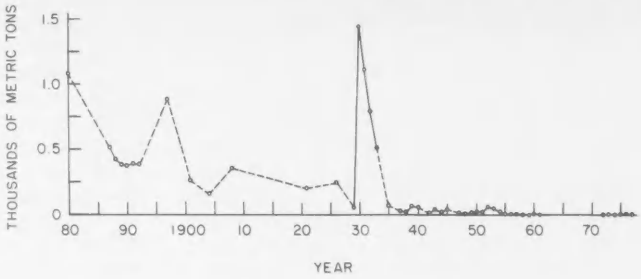

FIGURE 12.—Commercial landings of alewife in Delaware, 1880-1977.

depression, which created markets for a few years for cheap fish.

Establishment of water powered mills on all the tidal creeks, with their associated dams, may have contributed to the decline in landings, preventing spawning above the dams.

Sturgeon

Sturgeon was still fairly abundant in Delaware in the 1880's (Figure 13), producing 1,300 t (nearly 3 million lb). By the 1900's, however, they had declined to a low level, and yielded 45 t (<100,000 lb) annually thereafter. It is a tribute to the viability of the sturgeon that it has continued to produce small catches, despite its vulnerability. Fishermen in the early days may have contributed deliberately to the decline of the sturgeon stocks, by destroying them because they damaged nets. The great demand and high prices for caviar also undoubtedly had an effect.

Shad

Shad declined in landings much as sturgeon did in the early days, producing relatively small catches after about 1908 (Figure 14). In Delaware it produced somewhat increased catches in the mid-1940's, early 1950's, and early 1960's, but not as great during the days of the Second World War as in New Jersey, New York, and Connecticut. Like all anadromous species, shad was particularly vulnerable to adverse changes in the environment of rivers, but changing human tastes,

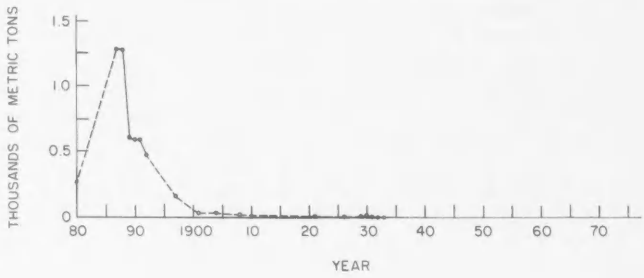

FIGURE 13.—Commercial landings of Atlantic sturgeon in Delaware, 1880-1932.

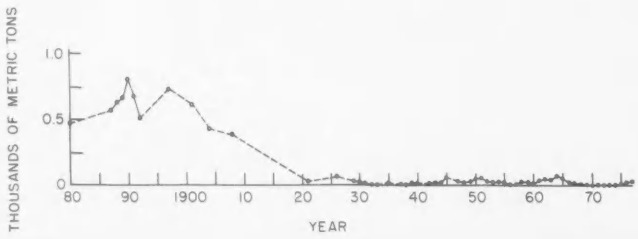

FIGURE 14.—Commercial landings of American shad in Delaware, 1880-1977.

highly seasonal demand, and the growing ease of trucking or flying shad from the south, where runs are much earlier, probably also played a part, as they did in New York (Medeiros 1974). Recreational fishing for shad in the Delaware River is growing (Grucela 1978) in landings and effort. The Delaware River stock is in good condition as compared with other rivers in the area.

Croaker

Croaker appeared later than weakfish in Delaware (Figure 15), reaching its peak in 1930 with about 500 t (slightly over 1 million lb). Thereafter it fell off irregularly, producing no catches after 1960 until 1975. Croaker, like weakfish, is a southern fish, and comes north of Chesapeake Bay only when conditions are particularly favorable, or when populations are high. Thus its abundance is likely to remain quite variable. The complete absence of croaker as a commercial resource during the 1960's and early 1970's may also have been caused by extensive use of DDT in estuaries, enhanced also by the stresses of living at the northern extreme of its range. Recovery in the mid-1970's may have been a delayed response to banning the use of this compound for mosquito control.

Hard Clam

Hard clam did not figure prominently in the catch in Delaware until after the Second World War (Figure 16) when stabilization of Indian River Inlet raised the salinity in the bay behind, and improved the environment for hard clam. It did not remain high for very long, however, and fell irregularly but steadily after 1951, when the maximum catch was about 414 t (912,000 lb) to 17 t (38,000 lb) in 1977, a drop of nearly 96%. It is probable that the decline was caused by a combination of overharvesting and pollution, which closed certain areas to clamming. Recreational clamming also is popular in Delaware (Miller 1978).

Spot

Spot is reported to have produced 295 t (650,000 lb) in Delaware in 1880, but was not reported again in catches until 1904 (Figure 17). This species is often caught by fishermen for their own

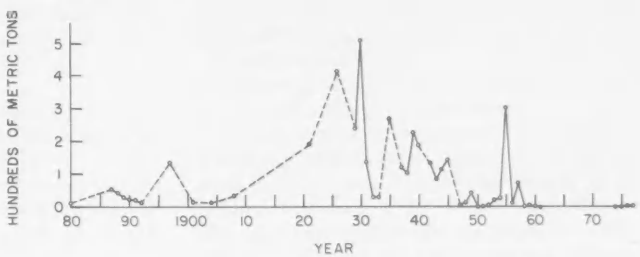

FIGURE 15.—Commercial landings of Atlantic croaker in Delaware, 1880-1977.

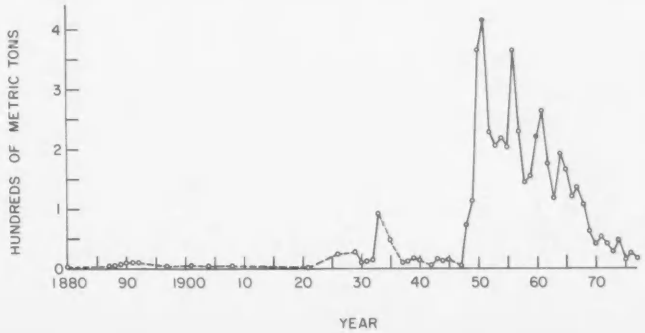

FIGURE 16.—Commercial landings of hard clam in Delaware, 1880-1977.

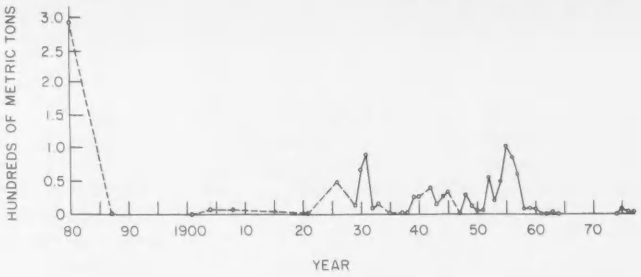

FIGURE 17.—Commercial landings of spot in Delaware, 1880-1977.

use, and is salted down for winter consumption. Such fish are not normally recorded in the catch. Existing records show that it reached a peak in 1931 and again in 1955, then fell off to nothing after 1963 until 1975. It is possible that spot also was affected by DDT in that period. Spot is an inshore species and, like croaker and other species, is near the northern limit of its range, thus is subjected sometimes to great stress when winter temperatures are low.

Striped Bass

Striped bass catches parallel those along other sections of the coast, declining to a low in the 1930's, then building up to a peak in the early 1970's, with rather wide fluctuations in between (Figure 18). There is little doubt that abundance has increased since the 1930's, but it is too early to say whether the recent decline is large enough to be of concern or simply reflects another temporary low in abundance. Striped bass probably once spawned in the Delaware River from Marcus Hook to below Wilmington where the river waters are normally between 1 and 5‰ in salinity. These waters are presently heavily polluted.

Regulation of the striped bass fishery has become a social-political matter, as the resource has grown in popularity as a sport fish. Recently, the Congress has allocated considerable sums for striped bass biological research, probably too late to do much good. If past history repeats itself, the resource will recover before the research produces much new knowledge. The State-Federal Fishery Management Board is putting together a coordinated coastwise research and management program, which may be of benefit if the states can get together on a uniform management program in the face of conflicting pressures. We will have to wait and see whether the past 50 yr have produced any accumulated wisdom that can be applied effectively.

Mullet

Mullet, *Mugil cephalus*, produced maximum landings in 1931 and fell off to low levels thereafter (Figure 19). Mullet may not have caught on as a popular fish in Delaware, and its brief upswing in the early 1930's may have been in response to the depression. There must be additional causes, however, for mullet has not been recorded in commercial catches since the early 1960's.

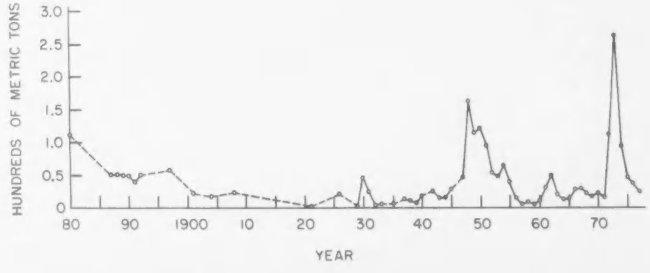

FIGURE 18.—Commercial landings of striped bass in Delaware, 1880-1977.

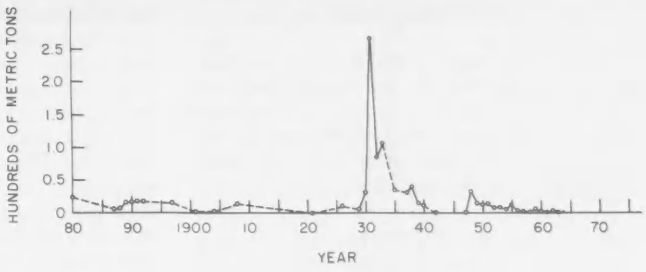

FIGURE 19.—Commercial landings of mullet in Delaware, 1880-1962.

American Eel

American eel, *Anguilla rostrata*, fell off to an all-time low in commercial landings in the 1940's, and since has built up slowly (Figure 20). Although it may have been affected by deterioration of the rivers, it does not spawn there, thus would not be affected as seriously as sturgeon, shad, or alewife. It is probably underexploited, and the recent modest size in landings in the last 30 yr may have been caused by increased markets in Europe and elsewhere.

White Perch

White perch has fallen off rather steadily since the 1880's, with major short rises in production in 1930, late 1940's, and 1958 (Figure 21). These fluctuations were probably caused by temporary upsurges in abundance caused by unusually good year classes. The decline in weakfish production generally has to be related to the decline in commercial fishing. There is no indication that the resource is in poor condition.

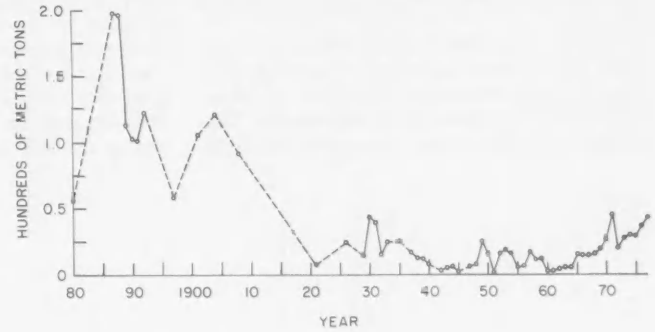

FIGURE 20.—Commercial landings of American eel in Delaware, 1880-1977.

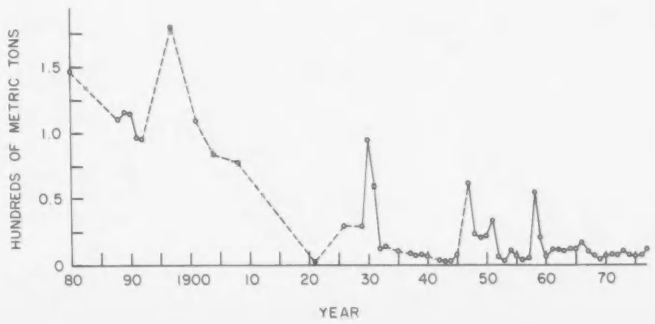

FIGURE 21.—Commercial landings of white perch in Delaware, 1880-1977.

FISHING GEARS

The principal gears used in Delaware were purse seines, gill nets, haul seines, pots, lines, and otter trawls. Except for otter trawls, these were mostly inshore gears, and took sturgeon, shad, alewife, weakfish, croaker, striped bass, and other anadromous or coastal species.

Purse Seines

Purse seines landed by far the greatest amounts of fishes in Delaware. The peak (Figure 22) was reached in 1953 at 165,000 t (somewhat over 360 million lb), the third largest of any state on the Atlantic coast, exceeded only by Virginia and New Jersey. Delaware led the states in menhaden landings in 1944-47, 1949, and 1952 and was second in 1950 and 1958. The fishery peaked temporarily in the 1940's, as did many fisheries toward the end of the war, but major landings were from 1953 to 1962, the decade of prosperity. The fishery collapsed soon after, and the last landings with purse seines were in 1966. Prior to the Second World War, the purse seine fishery was relatively small.

The purse seine fishery was directed at menhaden, and no other fishes were credited to this gear, although very small numbers of other species may have been taken occasionally. The collapse of this fishery was caused primarily by a reduction in abundance following the 1962 fishing year. The purse seine fishery in Virginia had been increasing in intensity during this period, and by 1963 relatively few fish survived the Virginia and North Carolina fisheries to migrate farther north. The effect was felt at all points north of Chesapeake Bay. Probably the only way of preserving the purse seine fisheries to the north, except on those rare occasions when large year classes or reduction in effort allowed some fish to migrate farther north, would have been to prohibit fishing south of Delaware or to place a minimum size on fishing to the south. Either alternative would be virtually impossible because southern fishermen would be certain to oppose it. The effect of such a law, if it could have been passed before a large industry developed in Chesapeake Bay and southward, would have been interesting to observe. It is possible, although of course not certain, that the decline might not have been as great.

Gill Nets

Four kinds of gill nets have been used in Delaware: drift, stake, anchor, and runaround. Drift gill nets were further broken down at times into shad, sturgeon, and other. For practical purposes, these can be broken down into fixed nets, drift nets, and runaround nets. Generally speaking, drift nets were set in slower waters farther downstream and took large quantities of weakfish and

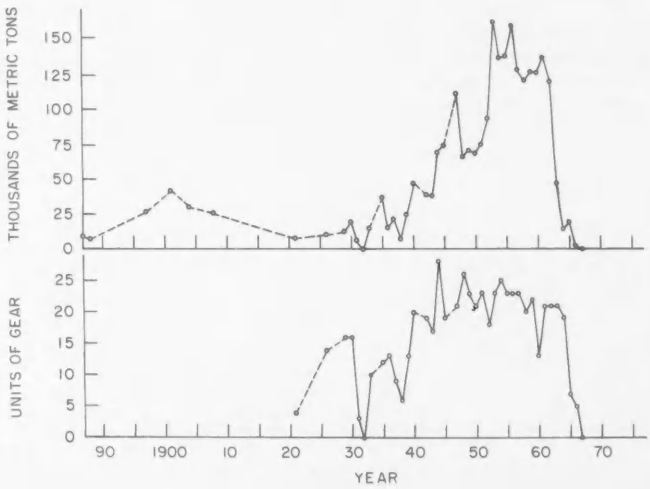

FIGURE 22.—Commercial landings by purse seines in Delaware, 1887-1966, and numbers of units of gear licensed.

croaker, among other fishes. Fixed nets were set for the most part farther upstream and took anadromous and freshwater species. Runaround nets also took mostly marine species, mullet when it was plentiful, but also weakfish, croaker, spot, and other fishes.

Landings from gill nets have declined rather steadily since the 1880's (Figure 23). The numbers of gill nets fell rather sharply to a low in the early 1940's, but have risen slowly since then. In general, numbers of gill nets have paralleled the catch, but whether they have remained about the same size is not known. Recent catches have been somewhat better than usual, as species like weakfish, striped bass, and certain others have shown up in increasing numbers off the coast.

In the beginning the greatest catch was sturgeon, making up >50% of the catch in 1887 and 1888. Sturgeon lost importance as time went on, dropping to seventh in importance by 1926, and was not a major species thereafter. American shad soon became first, but also dropped off fairly early, regaining first place in the mid-1930's, and holding this position almost every year until about 1951. Shad then dropped off again, regained first place in 1958, and was first until 1965 except for 1 yr. Since then it has fallen off to fourth or fifth place. Alewives ranked third in the early days, then slowly fell off, although in 1932 they ranked first. They are now relatively minor, and in several years in the late 1930's and early 1940's, and from 1958 to 1972, were caught in only 2 yr. Croaker became first in 1926 and retained that rank in most years until after 1945. Weakfish has fluctuated, but in general has increased in abundance, ranking second or third in most years since 1929, although it fell off in the early 1950's and again in the 1960's. In the 1970's it has ranked first most of the time. Striped bass has increased until recently, ranking first or second in 1958, and, except for a period of 5 yr in the late 1950's, has remained first or second until recently.

Other species have been prominent in landings occasionally, but have not remained among the primary species for long. Among these is mullet, first to third from 1931 to 1940, but absent from catches in most years since then. White perch ranked third to fifth until 1904, and did not regain this rank until 1960. Spot was second to fourth from 1939 to 1948, and again from 1952 to 1960,

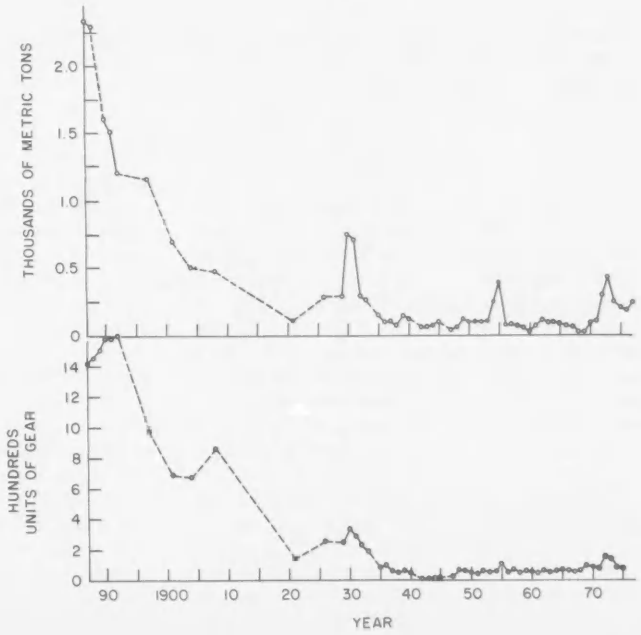

FIGURE 23.—Commercial landings by gill nets in Delaware, 1887-1977, and numbers of units of gear licensed.

even ranking first in 1956 and 1957. During the whole period gill net catches dropped from 22,700 t (>5 million lb) in 1887 to 45 t (<100,000 lb) in 1960, 1968, and 1969, then rose to 450 t (almost 1 million lb) in 1973. For most of the period, shad, weakfish, striped bass, and croaker, all relatively high-priced fishes, kept the fishery going, although until very recently, with decreasing numbers of fishes. It is difficult to escape the fact that the declining supply of weakfish was the primary reason for the decline of the gill net fisheries (Figure 11).

Haul Seines

Haul seines were a fairly important gear in the early days, reaching peak landings of 2,000 t (>4.4 million lb) in 1930 (Figure 24), but slowly and somewhat irregularly declining in production until the last net ceased operating in 1971 after landing <0.5 t (only 1,000 lb) of fishes. Weakfish again was the most important species most of the time, being exceeded by alewives in 1897, and in 1930 to 1933 inclusive. It is clear that weakfish was the mainstay of the haul seine fishery, and when it was gone the fishery did not survive for long. Haul-seining, however, has always been a part-time operation in spring according to Daiber (footnote 4).

Croaker also was important for a time, especially in 1926, 1929, and 1930, 1935 to 1942, 1945, 1955, and 1957. Shad was important from 1887 to 1904, white perch from 1887 to 1908. Striped bass was important in the 1880's and 1890's, showed up again from 1942 to 1951; common carp, *Cyprinus carpio*, was fairly important in 1897 to 1930, again in 1935 and 1950, 1951, and 1957; spot was important in 1926 and 1942; and mullet in 1948.

Pots

Pots were used for various species in Delaware, primarily for American eel, lobster, and blue crab. Later, considerable quantities of sea bass and conch, *Busycon* sp., were taken. Most of the catch, however, was blue crab, which peaked in 1957 and in 1975 (Figure 25). Obviously this fluctuation in blue crab abundance was real, dropping from 1,450 t (about 3.2 million lb) in 1957 to 110 t (<250,000 lb) in 1968, then climbing rather rapidly to 1,632 t (nearly 3.6 million lb) by 1975. This is the largest fishery in Delaware at present, but it is unlikely, in view of the variable nature of the resource, to remain high for long. Being near

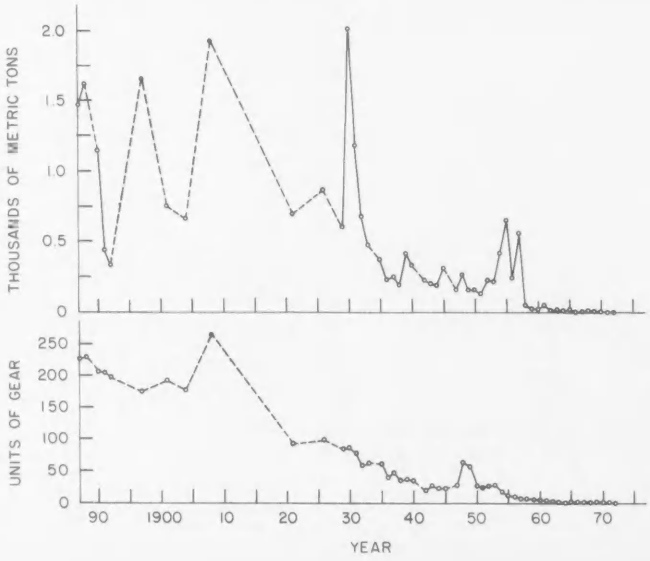

FIGURE 24.—Commercial landings by haul seines in Delaware, 1887-1971, and numbers of units of gear licensed.

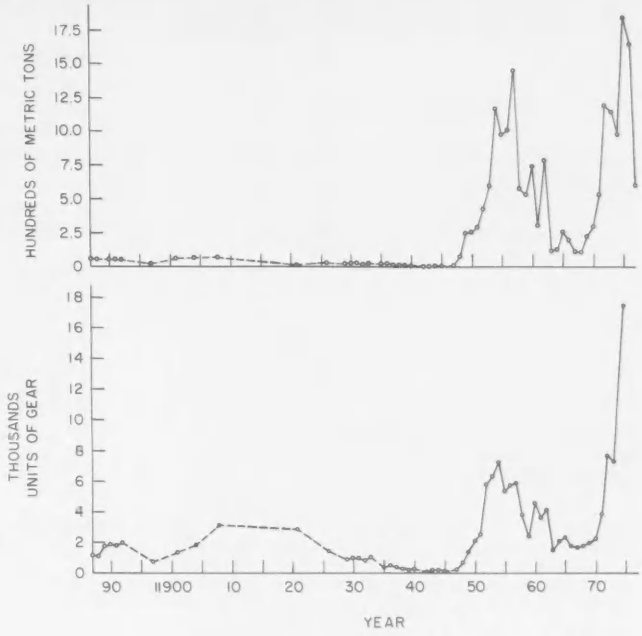

FIGURE 25.—Commercial landings by pots in Delaware, 1887-1977, and numbers of units of gear licensed.

the northern limit of its usual range, the blue crab is likely to be variable in abundance in Delaware.

Lines

Various kinds of line also were fished in Delaware from time to time. In addition to handlines, trawl lines, trotlines with baits, and longlines with hooks have been fished from time to time. From 1887 to 1926 inclusive, the kinds of line were not specified. In all years but one, however, weakfish was the largest catch. In 1926 crab made up about 85% of the catch, probably on trotlines with baits. From 1929 on, weakfish was an important, but variable component of the catch; tautog, *Tautoga onitis*, was important for a few years in the early 1930's; and croaker was an important, but variable component of the catch from 1930 to 1944. Striped bass was important from 1943 to 1945 and rose to first or second in rank in the 1970's. Trawl lines and later trotlines with hooks took almost exclusively cod, the first from 1929 to 1944, the second from 1960 to 1971. Trotlines with baits took blue crab in 1929, 1935, 1939 to 1951, and 1955 to 1960. Handlines were the only ones that have persisted, and their catches were almost entirely weakfish and striped bass in the 1970's (Figure 26). Once again, weakfish appears to have been the mainstay of the handline fishery.

Otter Trawl

The otter trawl fishery was relatively short lived in Delaware. It began in 1935, did not make catches again until 1940, reached its peak in 1948, and was over at the end of the 1966 season (Figure 27). It was an inshore fishery for the most part, taking mostly weakfish, summer flounder, scup, white perch, croaker, red hake, spot, butterfish, silver hake, striped bass, and squids. Over half the accumulated catch was weakfish, which substantiates the importance of this species to the fisheries of Delaware. The other main species, in the sense that they supported the fishery to the end, were summer flounder, butterfish, and striped bass. In the 1960's, recreational fishermen found an old law that prohibited trawling in Delaware Bay and put on pressure to enforce it. As already mentioned, this, with the decline in weakfish, was the final blow to the trawl fishery.

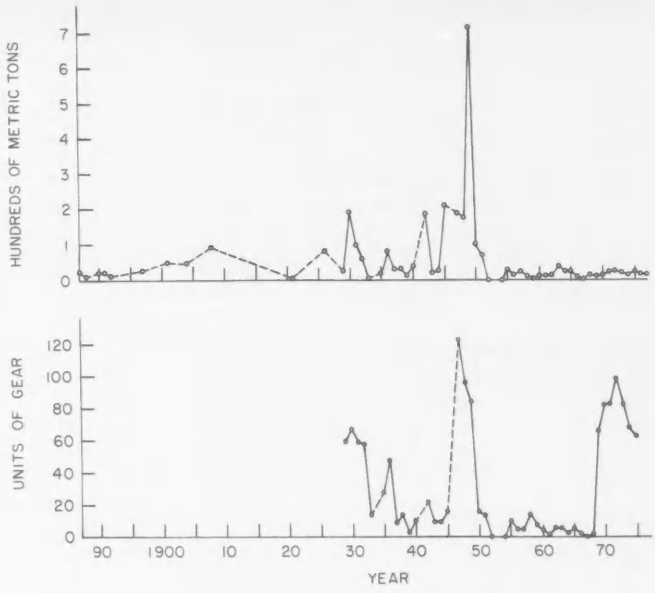

FIGURE 26.—Commercial landings by lines in Delaware, 1887-1977, and numbers of units of gear licensed.

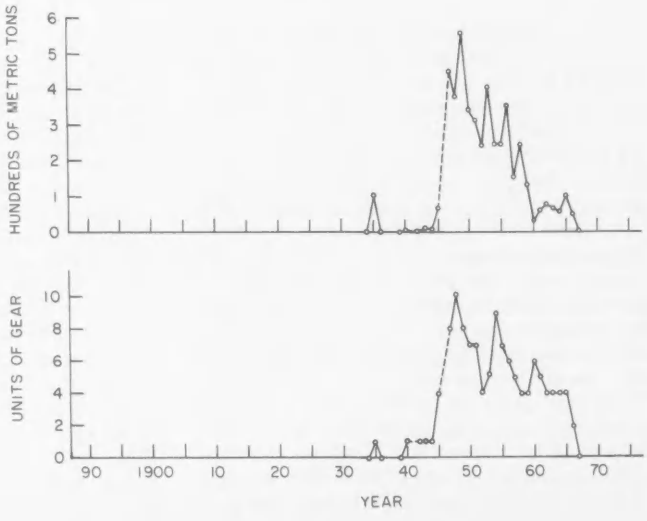

FIGURE 27.—Commercial landings by otter trawls in Delaware, 1935-66, and numbers of units of gear licensed.

Pound Net

Pound nets were not as important in Delaware as they were along most of the coast. They were used in Delaware mostly to catch horseshoe crab for manufacture into meal (Figure 28). Only 13.5% of the catch was fishes, and these were mostly alewife, white perch, carp, and catfish or bullheads (Family Ictaluridae). When horseshoe crab was no longer taken, pound nets quickly ceased operation. The last net was fished in 1938. In 1956 and 1957 pound nets were set again, but the catch was insignificant.

Oyster Dredges

Dredges were the main gear used to harvest oysters in Delaware, and they apparently took fair numbers prior to 1929 (Figure 29). There followed about a 15-yr period in which the catch was very

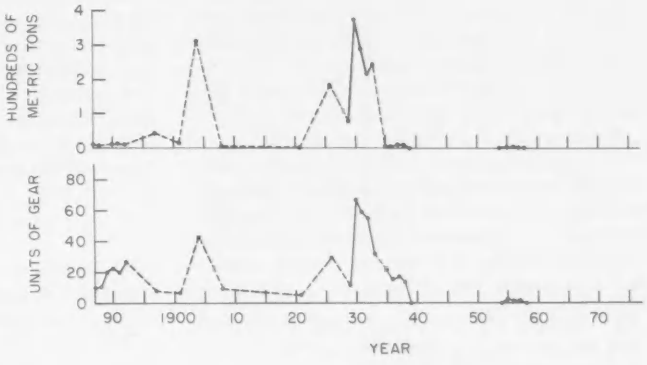

FIGURE 28.—Commercial landings by pound nets in Delaware, 1887-1957, and numbers of units of gear licensed.

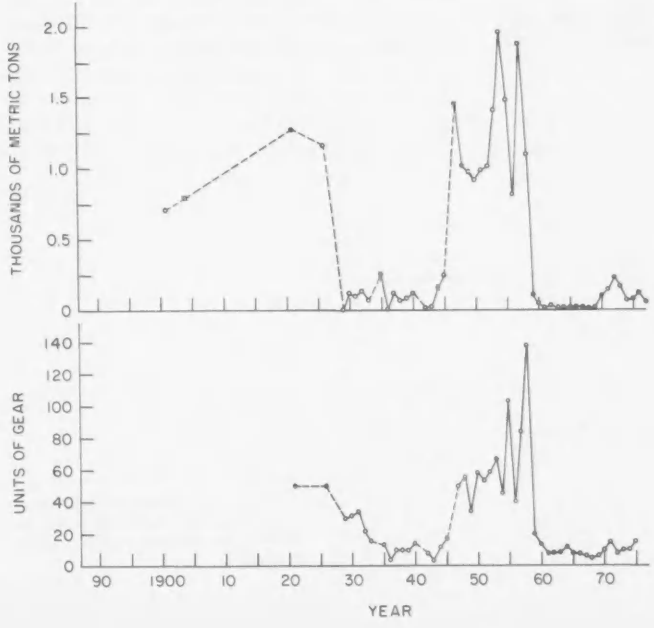

FIGURE 29.—Commercial landings by oyster dredges in Delaware, 1901-77, and numbers of units of gear licensed.

low, followed by the decade 1947 to 1958 when the industry was at its peak. After 1958 the industry almost collapsed, and it has not recovered. The harvest of oyster by tongs was much smaller, but somewhat similar through 1947. After 1947 there was no resurgence.

Maurer et al. (1971) made a survey of the oyster industry in Delaware Bay in 1968 and 1969. They found that Delaware Bay beds were badly depleted, but certain rivers in the vicinity showed potential as seed areas. One planted bed showed promise, suggesting that with proper management Delaware Bay could be rehabilitated and again produce oysters. The incidence of *Minchinia nelsoni* probably always was lower in the rivers than in the bay, and incidence on Delaware Bay beds was not as high as in the mid-1960's.

The hoped for increase had not occurred up to 1978, suggesting that no one was willing to take the risks, or had tried and failed. The present poor condition of oyster beds in Delaware Bay is caused by *M. nelsoni*, aggravated by general degradation of the environment. It is possible, but not certain, that with proper care the grounds could be restored to production.

Clam Dredges

Dredges were used to harvest hard clam and surf clam in Delaware. The first hard clam taken by dredge was recorded in 1901, but substantial numbers were not taken until 1929, when 360 t (nearly 800,000 lb) were caught (Figure 30). Catches dropped to much lower levels in 1931 and 1932, and remained fairly low until after the Second World War. This probably was at least partly caused by stabilization of Indian River Inlet, which raised the salinity in the Delaware Bay, and proved favorable for hard clam. Landings have been quite variable since, and the last hard clam listed as taken by this gear was in 1969.

Another short-lived fishery was dredging for surf clam, which began in 1956 and produced moderate catches until 1962, then ceased. Landings again were reported in 1969, peaked at 3,800 t (>8 million lb) in 1970, remained fairly high until 1974, but ceased in 1976. The fluctuations largely reflected where the boats were operating, as discussed earlier in the surf clam section.

Crab Dredges

Blue crab was first recorded as caught by dredges in Delaware in 1932. Catches were relatively small until the 1950's, when 1,700 t (>3.5 million lb) were recorded in 1950 and 1951 (Figure 31). Catches then dropped sharply, peaked again in 1957 at 770 t (about 1.7 million lb), and dropped to a very low level from 1964 to 1973, after which they picked up again but at a lower level.

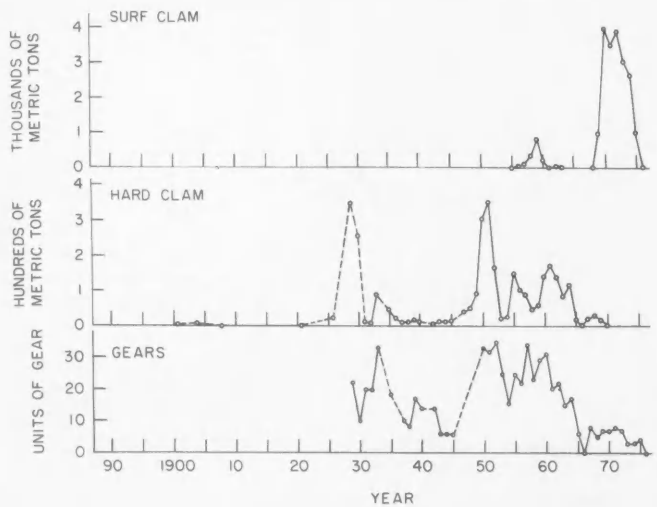

FIGURE 30.—Commercial landings by hard clam dredges in Delaware, 1901-69, and by surf clam dredges 1956-75, and numbers of units of gear licensed.

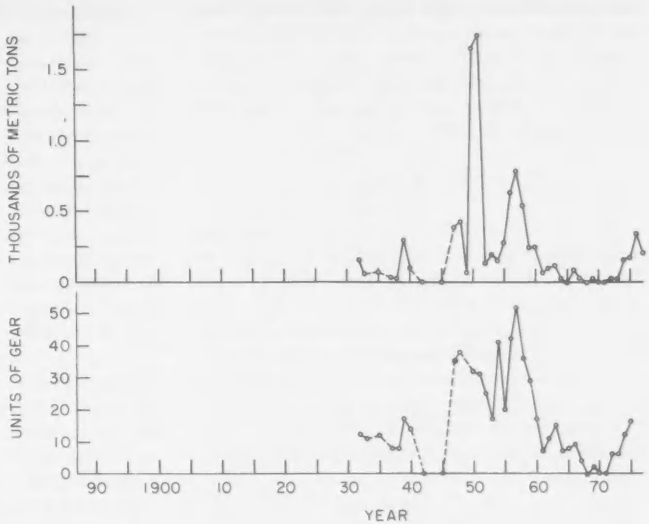

FIGURE 31.—Commercial landings by crab dredges in Delaware, 1932-77, and numbers of units of gear licensed.

Blue crab is highly variable in abundance in Delaware, and can not be expected to support a steady fishery.

Fyke Nets

Fyke nets were much more important in Delaware in the early days, reaching a low point in 1947, and fluctuating, more or less according to the abundance of fishes later (Figure 32). A low point in landings was reached in the 1940's, followed by peaks in 1955, 1964, and 1977, each at lower levels. Species composition of the catch has varied—catfish; white perch; American eel; sea bass; striped bass; alewife; flounders; yellow perch, *Perca flavescens*; and turtles making up most of the catch at various times.

Rakes

Most of the catch by rakes has been hard clam. Catches were insignificant in 1929 and 1930, and

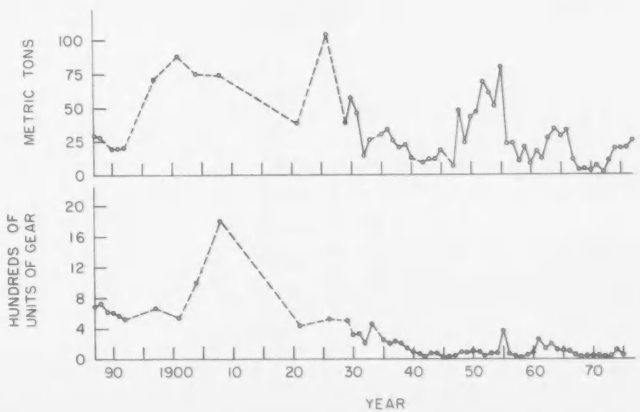

FIGURE 32.—Commercial landings by fyke nets in Delaware, 1887-1977, and numbers of units of gear licensed.

harvesting did not begin again until 1948 (Figure 33). Catches rose to a peak in 1953 at 215 t (about 474,000 lb), fell off to almost nothing by 1955, followed by an all-time high in 1956 of >300 t (683,000 lb). Subsequently, they have fallen off to 9 t (<20,000 lb) by 1977.

CONCLUSIONS

This history of the Delaware fisheries illustrates clearly the transient nature of marine resources generally in the Middle Atlantic Bight region, especially when effective controls on fishing are lacking. All of the major species in the region, with the possible exception of surf clam, are freshwater, anadromous, or coastal migratory species, and all have shown major fluctuations in abundance or availability. All are much less abundant in the region than formerly, and in nearly every case this can be attributed to overfishing. This, and the great variability in the supply of many of the major species, has led to a decline in the commercial fisheries, and a gradual takeover by recreational fishermen. Several major fisheries, e.g., purse seine, surf clam dredge, haul seine, otter trawl, and pound net fisheries, have ceased altogether.

Degradation of the coastal environment also has taken a toll, although this cannot be documented clearly. However, it is fairly clear that dams and pollution of coastal streams have affected spawning of anadromous species, and these have suffered most. Mitigation of pollution and clearing of obstructions from waterways should improve the situation.

The future is uncertain. Many of the species cannot be helped very much unless cooperation with other states is improved. This is underway through the State-Federal Fishery Management Board, but it is too early yet to tell how much this will improve the situation. Menhaden is unlikely to come back unless effective steps can be taken to increase mesh size or otherwise reduce the catch of small fishes in Virginia and North Carolina. Even if that unlikely alternative is accomplished, it probably would be difficult or impossible to reestablish a reduction plant because environmental laws in Delaware would prevent it. Weakfish was the principal mainstay of the food fish industries in Delaware, and its present value to recreational fishermen in the State makes it unlikely that a commercial fishery will start again. The other species are even less likely to support major commercial fisheries.

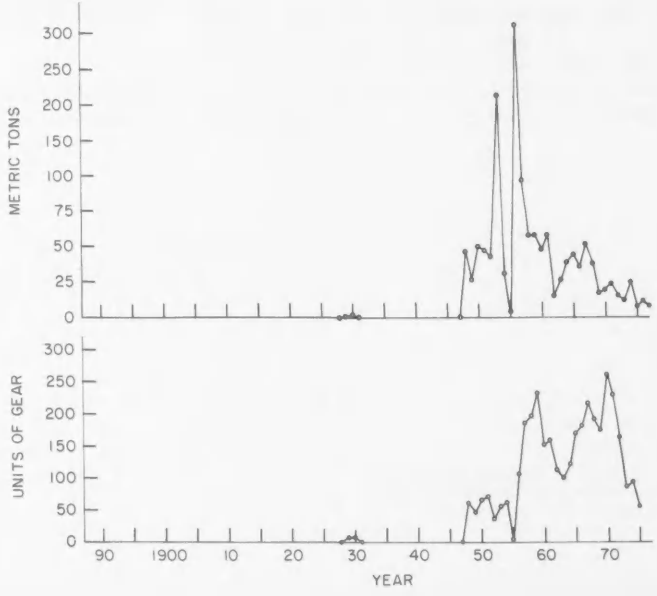

FIGURE 33.—Commercial landings by rakes in Delaware, 1929-77, and numbers of units of gear licensed.

The remaining species are shellfishes, mainly surf clam, blue crab, American oyster, and hard clam. The future of the surf clam resource will depend upon how successful the Mid-Atlantic Council can be in developing adequate enforcement measures, and on the ability of the states to develop parallel management plans. Blue crab will probably continue to be highly variable in production, but should be able to support a fairly prosperous fishery at times. Oysters might be able to come back from their present reduced level if adequate attention is paid to modern methods of culture. Hard clam probably can support a modest fishery if the environment of the coastal bays can be preserved and enhanced.

As a whole, it appears that the commercial fisheries of Delaware will remain small, and that they will be largely shellfisheries. Recreational fishing probably will continue to take increasing numbers of the total catch of finfishes. Whether the recreational fisheries can be managed to maintain the yield will depend upon how the states can cope with this problem.

LITERATURE CITED

COLLINS, J. W.
1887. Delaware and its fisheries. Part IX in The fisheries and fishery industries of the United States, by G. B. Goode. Sect. II. Misc. Doc. 124, Senate of the U.S. 1881-'82, vol. 7:407-419.

DEUEL, D. G.
1973. 1970 Salt-water angling survey. U.S. Natl. Mar. Fish. Serv., Curr. Fish. Stat. 6200, 54 p.

GRUCELA, B.
1978. In retrospect...Delaware River shad fishing. Pa. Angler 47(5):8-13.

GUNTER, G.
1975. An example of oyster production decline with a change in the salinity characteristics of an estuary, Delaware Bay 1800-1973. (Abstr.) Proc. Natl. Shellfish. Assoc. 65:3.

JOSEPH, E. B.
1972. The status of the Sciaenid stocks of the Middle Atlantic coast. Chesapeake Sci. 13:87-100.

JUNE, F. C., AND J. W. REINTJES.
1957. Survey of the ocean fisheries off Delaware Bay. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 222, 55 p.

MAURER, D., L. WATLING, AND R. KECK.
1971. The Delaware oyster industry: a reality? Trans. Am. Fish. Soc. 100:100-111.

MEDEIROS, W. H.
1974. Management and rehabilitation of the Hudson River shad fishery. N.Y. Sea Grant Program and N.Y. State Assembly Scientific Staff, 65 p.

MILLER, R. W.
1978. Marine recreational fishing in Delaware. Bureau of Archives and Records, Hall of Records, Dover, Del., Doc. 40-05/78/01/18, 28 p.

PARR, A. E.
1933. A geographic-ecological analysis of the seasonal changes in temperature conditions in shallow water along the Atlantic coast of the United States. Bull. Bingham Oceanogr. Collect. Yale Univ. 4(3), 90 p.

PERLMUTTER, A.
1959. Changes in the populations of fishes and in their fisheries in the Middle Atlantic and Chesapeake regions, 1930 to 1955. Trans. N.Y. Acad. Sci., Ser. II, 21:484-496.

PILEGGI, J., AND B. G. THOMPSON.
1978. Fishery statistics of the United States 1975. U.S. Natl. Mar. Fish. Serv., Stat. Dig. 69 (and previous numbers in this series), 418 p.

PRICE, K. S.
1978. Advances in closed (recirculated) system mariculture. Rev. Biol. Trop. 26 (Suppl. 1):23-43.

REINTJES, J. W., AND C. M. ROITHMAYR.
1960. Survey of the ocean fisheries off Delaware Bay—Supplement Report, 1954-57. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 347, 18 p.

ROUNSEFELL, G. A., AND W. H. EVERHART.
1953. Fishery science: its methods and applications. Wiley, N.Y., 444 p.

WATERS, O. D., JR.
1967. Oceanographic atlas of the North Atlantic Ocean, Sect. II, Physical properties. U.S. Nav. Oceanogr. Off., Publ. 700, 300 p.

ASSIMILATION EFFICIENCY AND NITROGEN EXCRETION OF A FILTER-FEEDING PLANKTIVORE, THE ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS* (PISCES: CLUPEIDAE)

EDWARD G. DURBIN AND ANN G. DURBIN[1]

ABSTRACT

Experiments were carried out at 20° C with adult Atlantic menhaden, *Brevoortia tyrannus*, to follow the time course of changes in feces elimination rate, assimilation efficiency, nitrogen excretion rate, and oxygen:nitrogen ratios during and after a 7-hour period of feeding on the diatom *Ditylum brightwelli*. Assimilation efficiency for wild zooplankton dominated by *Acartia tonsa* is also reported.

The elimination of a meal was exponential (mean = 0.366/hour) and thus meals of different size reached the same stage of digestion at the same time. Changes in stomach contents and evacuation rates with time were calculated using the model of Elliott and Persson. These corresponded closely with observed changes in feces elimination rates following a meal. Assimilation, as indicated by the patterns of nitrogen excretion, and the elimination of a meal were rapid: 50% of the exogenous nitrogen excretion occurred within 1 or 2 hours after 50% of the meal was ingested; 50% of the feces were eliminated within a mean of 5.7 hours after the midpoint of feeding.

Mean carbon, nitrogen, and caloric assimilation efficiencies for *D. brightwelli* were 86.4, 92.4, and 89.5%; for zooplankton these were 86.7, 91.3, and 87.7%, respectively. Assimilation efficiencies decreased when fecal elimination rates declined below 0.3 mg dry weight/g dry weight per hour. This resulted in lower assimilation at the beginning and end of each experiment, and a slight decrease in the overall assimilation efficiency in low ration experiments, where the fecal elimination rates were also low.

Nitrogen excretion consisted of 69.6% ammonia and 30.4% dissolved organic nitrogen. The mean excretion rate of fish unfed for 36 hours (10.72 μg nitrogen/g dry weight per hour) increased as much as 17-fold when the fish were digesting and assimilating the food. Exogenous nitrogen excretion was a constant proportion of the ingested and the assimilated rations (61.6 and 65.5%, respectively).

Oxygen:nitrogen ratios indicated that Atlantic menhaden use protein as a metabolic fuel at all times. The mean oxygen:nitrogen (28.2) of fish unfed for 36 hours decreased to values as low as 5.0 during feeding.

In the development of an energy budget for fish it is necessary to determine the proportion of the ingested ration which is lost in the feces and the excretory products. The remainder represents physiologically useful energy available for growth and metabolism.

Here we examine digestion rates, assimilation efficiency, nitrogen excretion rates, and oxygen:nitrogen (O:N) ratios of adult Atlantic menhaden, *Brevoortia tyrannus*, a filter-feeding planktivore. Since Atlantic menhaden normally feed for a prolonged period each day, the experiments were designed to permit observations on the fish before, during, and after a 7-h feeding period during which food was made available at a constant rate. This study is part of a larger effort to determine the energy budget of Atlantic menhaden in Narragansett Bay, R.I.

METHODS

All experiments were carried out on a school of 12 Atlantic menhaden, with a mean wet weight of 302 g, dry weight of 101 g, and fork length of 26 cm. Experiments were carried out during 26 July-9 September 1977 at a temperature of 20.0 ± 1.0° C and a salinity of 31‰. Details of the procedures used for maintenance of the fish and for carrying out the experiments are given in Durbin et al. (1981).

Before an experiment the tank was thoroughly cleaned and the inflowing water was filtered through a GAF[2] polypropylene bag filter of nominal 5 μm pore size. The fish were deprived of food for 36 h to eliminate the remains of the previous meal. The experiment began with a measurement of the excretion rate of the unfed fish between 0600

[1]Graduate School of Oceanography, University of Rhode Island, Kingston, RI 02881.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted June 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

and 0800 h. Plankton was then siphoned into the tank at a constant rate over a 7-h period from about 0800 to 1500 h. At intervals prior to, during, and for about 20 h after the feeding period, respiration rates and voluntary swimming speeds were measured (Durbin et al. 1981), and samples of the tank water were collected for determination of ammonia and dissolved organic nitrogen (DON) excretion rates. Feces were periodically siphoned from the tank during the feeding period and for 41 h thereafter for the determination of assimilation efficiency. The tank was briefly flushed with filtered seawater at the end of the feeding period to reduce the ammonia concentration. Control measurements on the tank and tank water with and without plankton, demonstrated that these did not measurably effect ammonia or dissolved oxygen concentrations during the experiments.

Seven experiments were carried out using cultures of the solitary diatom *Ditylum brightwelli*, and three using Narragansett Bay zooplankton consisting mainly of adult *Acartia tonsa* and a small number of unidentified crab zoeas. Details of the culturing and processing of the *D. brightwelli* during experiments are given in Durbin et al. (1981). Narragansett Bay zooplankton were collected with 0.5 m diameter, 300 μm mesh nets on the day before an experiment and maintained alive in 1.2 m diameter tanks overnight.

During each experiment the plankton was concentrated into seven equal batches of about 18 l. Each batch was then siphoned into the tank over a 1-h period, providing an approximately constant input of food over the 7-h period without greatly changing the volume of the tank (1,400 l). Each batch of phytoplankton was subsampled for determination of C and N (Durbin et al. 1981). Each hourly batch of zooplankton was concentrated onto a 100 μm mesh and weighed just before use. A subsample of this was removed for determination of the dry weight:wet weight ratio, C and N content (Hewlett-Packard Model 185B CHN Analyzer), ash (combustion at 475° C for 4 h), caloric (Parr adiabatic bomb calorimeter), and chitin (Windell 1966) content. The remaining sample was dispersed in about 18 l of water and siphoned into the tank. By changing the concentration of plankton in the batches, we obtained different concentrations of food in the tank and different ration sizes. Turbulence produced by the swimming of the fish kept the water and plankton in the tank well mixed at all times.

Feces settled to the bottom of the tank, and were collected at 1-6 h intervals depending on the rate at which they were eliminated. Feces were gently siphoned into a plastic bucket and allowed to settle; the water was then aspirated off, and the feces were briefly rinsed with a little distilled water and transferred to preweighed aluminum dishes. Fecal pellets formed cohesive, cylindrical rods; the loss of material during collection and concentration was nominal. These dishes were then freeze-dried and reweighed to determine the dry weight of the feces. Each sample of feces was subsequently analyzed for carbon and nitrogen (3 replicates), ash (4-8 replicates), and calories (4 replicates). Each sample of feces from the phytoplankton experiments was also analyzed in triplicate for particulate silicon (Durbin 1977).

Samples for dissolved nitrogen analysis were siphoned from the tank into a clean, acid washed container, and then filtered through prerinsed glass fiber filters. The sampling interval was 1-4 h, depending on the excretion rate. All determinations were carried out in triplicate.

Ammonia determinations were carried out immediately with a modification of the method of Solorzano (1969), using 10 ml samples which were incubated in the dark for 4 h for color development. The range of values for 3 replicates was <0.1 μM of ammonia.

Total dissolved nitrogen was determined using the alkaline persulphate method of D'Elia et al. (1977). Nitrate formed during digestion of the samples was determined using a Technicon AutoAnalyzer II. At the same time, nitrate, nitrite, and ammonia concentrations were also determined on noncombusted subsamples using the AutoAnalyzer. These concentrations were subtracted from the total dissolved nitrogen determined from the persulphate digestion to give a measure of DON. Ammonia concentrations of the samples which had been frozen were always very similar to the concentrations determined from fresh samples immediately after collection. The range of values for three replicates of each measurement of total dissolved N was ≤ 0.5 μM N.

Excretion rates of the nonfeeding fish were low, and thus changes in total dissolved nitrogen concentration in the tank water were small. Although the ammonia excretion rate could always be satisfactorily determined, the greater errors inherent in the DON determination made it impossible to accurately measure DON excretion except during and soon after feeding, when the N excretion rates were high. During feeding the increase in NH_3

and DON concentrations in the tank was approximately linear, and linear regressions were calculated to estimate the excretion rates. The ratio of the DON:NH_3 regression slopes was similar in all experiments (overall means $\Delta DON/\Delta NH_3$ = 0.437, σ = 0.088). We assumed that this average value would provide the best estimate of DON excretion in both feeding and nonfeeding fish, and therefore multiplied the observed NH_3-N excretion rates by 0.437 to calculate DON-N excretion.

The Atlantic menhaden did not excrete any measurable quantities of nitrate, nitrite, or dissolved silicon. The latter was measured because of the large amounts of particulate silicon in the phytoplankton used as food. Nitrate, nitrite, and silicate were determined in triplicate on selected samples using methods described in Strickland and Parsons (1972).

Assimilation efficiency was calculated in two ways: by calculating the overall assimilation efficiency of C, N, and calories, and by following the time course of changes in the assimilation efficiency during each experiment. Both methods were based on the assumption that all of the feces were quantitatively collected.

The overall assimilation of C, N, or calories was determined by subtracting the total amount of each of these constituents that remained in the feces, from the amount in the food for each experiment. The C assimilation efficiency (percent), for example, was calculated:

$$\text{C assimilation} = \frac{C_{food} - C_{feces}}{C_{food}}(100). \quad (1)$$

In the second method, assimilation was calculated separately for each sample of feces. Since silicon (Si) was not absorbed by the fish, the Si content of each sample of feces was used to calculate the quantity of food (C, N, calories) which corresponded to each fecal sample. This was done by using the C:Si, N:Si, and calories:Si ratios of the food for each experiment, which were calculated from the measurements of the C, N, and calories in the food, and the total Si content of the feces. The assimilation efficiency was then determined in a manner analagous to Equation (1), using the back-calculated amount of C, N, and calories in the food which corresponded to each fecal sample, and the actual amount of C, N, and calories remaining in the sample.

The assumptions that all of the feces were collected quantitatively, and that Si was not absorbed by the fish, were verified in a phytoplankton experiment in which Si was used as a tracer. Subsamples of the phytoplankton were centrifuged and the Si content of the freeze-dried pellets then determined. This gave an estimate of 1.87 g for the total Si in the ration, which was very similar to that actually collected in the feces, 1.98 g.

A small but unknown amount of seawater remained interstitially within the pellets of both the phytoplankton and the feces, the salt content of which may have contributed to the estimates of ash content (Table 1). Because of this it was not possible to use ash content as a tracer to calculate assimilation efficiency. However, it should be noted that since the calculations of assimilation were based on direct measurements of C, N, and Si in the food and feces, they were not affected by the presence of trace amounts of seawater in the samples.

Nitrogen excretion and feces elimination by Atlantic menhaden are reported per gram dry weight, as micrograms N per gram dry weight per hour and milligrams per gram dry weight hour, respectively. It should be noted that measurements of oxygen consumption by the Atlantic menhaden during these experiments were reported in Durbin et al. (1981) as milligrams O_2 per gram wet weight per hour, to conform to the usual manner of reporting respiration rates in the literature.

RESULTS

The chemical composition of Atlantic menhaden, zooplankton, and *D. brightwelli* differed considerably (Table 1). Atlantic menhaden contained more C and calories, and less ash, per gram dry weight than the plankton, and were intermediate in N content between *D. brightwelli* and zooplankton. The composition of the fecal pellets was considerably altered from that of the food (Table 1). Atlantic menhaden assimilated N more efficiently than C, causing the C:N ratios of the fecal pellets to be higher than in the food.

The total dry weight of plankton fed to the 12 fish in each experiment ranged from 7.20 to 17.67 g of zooplankton, and 9.60 to 94.79 g of phytoplankton (Table 2). However, since the chemical composition of Atlantic menhaden differs from that of the plankton, the food rations are equivalent to different percentages of Atlantic menhaden dry weight, C, N, and calories. For example, the phytoplankton rations represented from 0.79% to

TABLE 1.—Chemical composition (mean ± σ) of *Brevoortia tyrannus*, plankton food organisms, and *B. tyrannus* fecal pellets.

Item	Dry wt as % of wet wt	Percent of dry weight					C:N	kcal/g dry wt	kcal/g ash-free dry wt
		Carbon	Nitrogen	Chitin	Silicon	Ash[1]			
B. tyrannus[2]	33.4±1.80	56.61±3.18	8.03±0.78	—	—	10.94±1.40	7.05	6.238±0.481	7.002±0.450
Zooplankton[3] mostly *Acartia tonsa*	10.86±0.20	40.05±2.34	10.91± .86	5.42±0.69	—	19.96±3.81	3.67	4.278± .161	5.348± .059
Chitin	—	39.37± .89	5.88± .17	—	—	—	6.70	—	—
Phytoplankton[4]: *Ditylum brightwelli*	—	18.52± .19	3.04± .05	—	9.28±0.16	55.24± .37	6.09	1.872± .072	4.179± .160
Fecal pellets[5]:									
Zooplankton	—	10.34±1.20	1.85± .34	—	—	72.3±2.14	5.59	1.013± .037	3.666± .297
Phytoplankton	—	9.29±1.34	.80± .11	—	25.7±7.35	74.6±1.20	11.61	.715± .042	2.818± .111

[1]May be an overestimate for plankton and fecal pellets; see text.
[2]Dry weight was determined on experimental fish; other constituents estimated from measurements on Atlantic menhaden collected from Narragansett Bay, R.I. (Durbin et al. unpubl. manuscr.).
[3]Mean ± σ of Experiments 1-3.
[4]*D. brightwelli* from Experiment 7; mean ± σ of four replicate determinations.
[5]Mean ± σ from Experiments 1-3 (zooplankton) and 4-10 (phytoplankton).

TABLE 2.—Food rations fed to 12 Atlantic menhaden.

Food type	Experiment no.	Duration of feeding (h)	Feeding rate[1] (mg food/g dry wt fish per h)	Food rations[2]				
				Dry weight[1]		Carbon (% of fish)	Nitrogen (% of fish)	kcal (% of fish)
				g	% of fish			
Zooplankton mostly *Acartia tonsa*	1	5.6	2.61	17.67	1.46	0.97	1.81	0.96
	2	8.1	1.19	11.58	.96	.71	1.39	.68
	3	3.8	1.55	7.20	.59	.42	.82	.41
Phytoplankton *Ditylum brightwelli*	6	7.1	10.99	94.79	7.80	2.56	3.01	2.35
	4	7.3	9.79	86.93	7.15	2.35	2.60	2.15
	5	7.0	7.93	67.46	5.55	1.82	2.13	1.67
	9	6.7	3.39	27.64	2.27	.75	.75	.68
	7	6.8	2.51	20.76	1.71	.56	.61	.51
	8	6.9	1.84	15.43	1.27	.42	.42	.38
	10	6.9	1.14	9.60	.79	.26	.29	.24

[1]Dry weight of zooplankton was measured in each experiment. Phytoplankton dry weight was estimated from C measurements in each experiment, and the conversion factor milligram C = 0.1852 (mg dry wt) (Table 1).
[2]Based on 12 fish = 1,212 g dry weight, 686.1 g C, 97.3 g N, and 7,560 kcal.

7.8% of the Atlantic menhaden dry weight, but only 0.26% to 2.56% of the estimated carbon content of the fish.

Each of the 12 fish was assumed to have obtained the same proportion (1/12) of the plankton added to the tank. This appeared reasonable since they were of similar size and swam at the same average speed during feeding (Durbin et al. 1981), and thus filtered similar volumes of water.

In the zooplankton experiments the duration of the feeding period was variable because of a problem caused by crab zoeas present in low numbers in the plankton. It was apparent that the sharp, 5 mm spines of these zoeas irritated the gill rakers of the Atlantic menhaden, because in three of four experiments attempted, the fish fed normally at first, then stopped feeding and began shaking their heads and repeatedly flaring their gill rakers. They stopped this unusual behavior as soon as the zoeas were washed out of the tank with filtered seawater. The fish were not satiated, since trial experiments demonstrated that once the zoeas were removed, the fish would feed readily on salmon food. The number of zoeas was least in Experiment 2, and in this instance the fish fed in their normal manner for as long as zooplankton was made available, 8.1 h. Because of these problems, only total assimilation efficiency will be reported from the zooplankton experiments.

Feces Elimination

In the phytoplankton experiments, feces began to appear about 2.4 h after the beginning of feeding (Table 3, column 2). The rate of elimination continually increased during the feeding period. The peak rates increased with increasing meal size, and occurred during the first 1 or 2 h following feeding (Figures 1, 2, 3). The elimination of feces began an approximately exponential decline 2 or 3 h after the end of feeding (Figure 1). With the exception of Experiment 6, these rates were all similar (overall $\bar{X}$ = 36.6%/h, or 38.1%/h if Experiment 6 is excluded) (Table 3, column 8). The exponential period lasted until about 14 h after the end of feeding, after which elimination continued at a low, nearly constant rate for the next 27 h (Figures 2, 3).

One consequence of the exponential elimination of the feces was that different sized rations

TABLE 3.—Feces elimination and nitrogen excretion of a school of 12 Atlantic menhaden, in relation to a 7-h period of feeding on the diatom *Ditylum brightwelli*, where time t_0 = the beginning, $t_{0.5}$ = the midpoint, and t_1 the end of the feeding period. At $t_{0.5}$, 50% of the ration has been ingested. Column numbers, in parentheses, are for text reference.

	Elapsed time (h)						
	After t_0	After $t_{0.5}$		After t_1			
Experiment no. (1)	Elimination begins (2)	50% Si eliminated (3)	50% N excreted (4)	90% Si eliminated (5)	90% N excreted (6)	Elimination rate ≥0.3 mg/g per h (7)	Exponential decline in elimination rate (per h) after t_1 (8)
6	2.0	5.5	2.3	10.0	2.9	13	−0.275
4	2.0	5.8	1.9	6.6	1.3	10	− .363
5	1.4	5.7	1.3	7.5	2.8	10	− .344
9	3.9	5.8	1.1	8.9	3.3	6	− .372
7	2.5	5.3	1.0	6.6	5.3	6	− .406
8	2.2	6.1	1.0	7.7	.7	7	− .392
10	2.6	6.0	1.5	7.0	.8	5	− .409
Mean ± σ	2.4 ± 0.8	5.7 ± 0.3	1.4 ± 0.5	7.8 ± 1.3	2.4 ± 1.6		−.366 ± .046

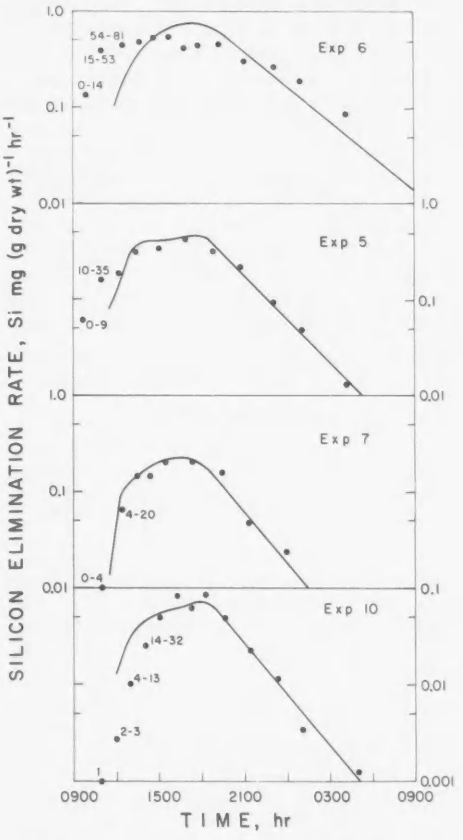

FIGURE 1.—Silicon elimination rate (circles) of a school of 12 *Brevoortia tyrannus*, during and after a 7-h (0800-1500 h) period of feeding on the diatom *Ditylum brightwelli*. Curve representing the calculated stomach evacuation rate is fitted to the feces elimination data; further explanation in text. Numbers refer to the elapsed time (minutes) in the feeding period when food corresponding to the fecal sample was ingested.

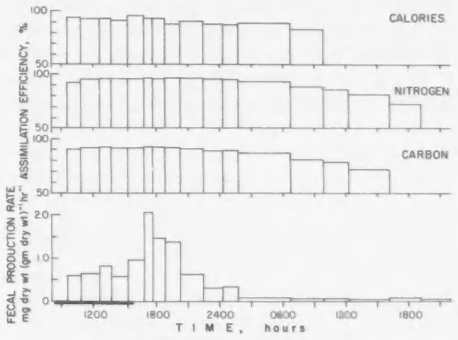

FIGURE 2.—Experiment 4 (high ration, Table 4). Changes in the fecal elimination rate of 12 *Brevoortia tyrannus*, and carbon, nitrogen, and caloric assimilation efficiency during and after a 7-h period of feeding (dark line on the *x*-axis) on *Ditylum brightwelli*.

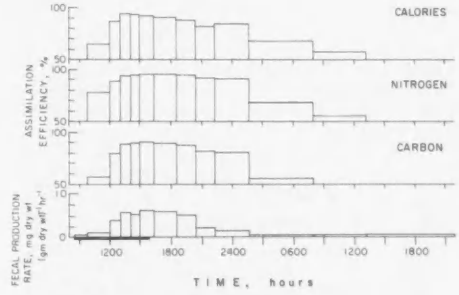

FIGURE 3.—Experiment 7 (low ration, Table 4). Symbols are as in Figure 2.

reached the same stage of elimination (i.e., 50%, 90%) at about the same time (Table 3, columns 3, 5).

Particulate Si in the feces was used to trace the passage of phytoplankton through the gut, since Si was not digested by the fish. Elimination of the experimental meal was rapid; 50% of the Si from the food was recovered in the fecal pellets within an average of 5.7 h after the midpoint of the feeding period (the time at which 50% of the food had been ingested) (Figure 4; Table 3, column 3). Because of the exponential decline in feces production following feeding, Si from the second half of the ration was egested more slowly, particularly the final 10%. Ninety percent of the Si in the food was recovered within a mean of 7.8 h after the end of feeding (Figure 4; Table 3, column 5) and a mean of 94.3% was recovered by 10 h after the end of feeding. Much of the fecal material eliminated during the next 31 h appeared to have sloughed from the gut since the C:Si ratios were higher in these samples. The amount of Si released during the interval between 14 and 41 h after the end of feeding was small, corresponding on the average to the food ingested during the final 10 min of the 7-h feeding period.

Assimilation Efficiency

The assimilation efficiency was high and similar for both phytoplankton and zooplankton (Table 4, columns 3, 4, 7). In the phytoplankton experiments, there was a slight positive trend between assimilation and increasing meal size, except in the largest ration experiment. In this experiment, assimilation appeared to be reduced.

It is not known whether Atlantic menhaden are able to digest chitin. The chitin content of the

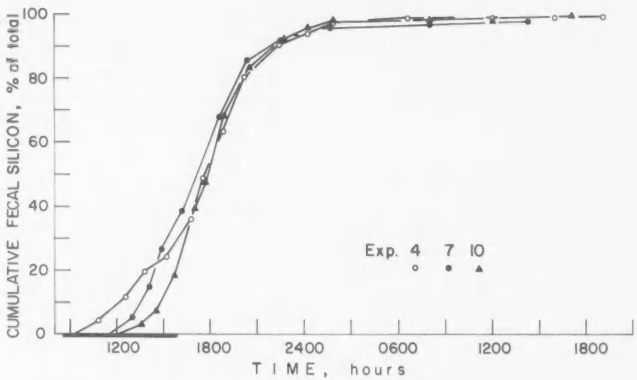

FIGURE 4.—Cumulative fecal silicon eliminated by 12 *Brevoortia tyrannus* in Experiments 4, 7, and 10 during and after the 7-h feeding period.

TABLE 4.—Assimilation efficiency of *Brevoortia tyrannus*, and the percentage of the total feces which were eliminated at a rate ≤0.3 mg/g dry weight per h. A) Overall assimilation efficiency. B) Assimilation during the period when fecal production was ≥0.3 mg/g dry weight per h. C) Calculated assimilation after subtraction of the chitin C and N from the total. Column numbers, in parentheses, are for text reference.

Food type (1)	Experiment no. (2)	kcal A (3)	Assimilation efficiency (%) Carbon A (4)	Carbon B (5)	Carbon C (6)	Nitrogen A (7)	Nitrogen B (8)	Nitrogen C (9)	% of total elimination ≤0.3 mg/g per h (10)
Zooplankton	1	89.01	86.55	—	91.79	90.23	—	93.25	—
mostly	2	88.19	87.09	—	91.10	91.78	—	94.01	—
Acartia	3	85.80	86.39	—	91.39	91.88	—	94.72	—
tonsa	Mean ± σ	87.67 ± 1.67	86.68 ± 0.37		91.43 ± 0.35	91.30 ± 0.93		93.99 ± 0.74	
Phytoplankton	6	89.76	86.86	87.23	—	92.48	92.57	—	10.81
Ditylum	4	92.20	91.08	91.49	—	95.28	95.53	—	7.50
brightwelli	5	—	89.39	89.91	—	94.47	94.81	—	9.02
	9	—	86.99	89.15	—	92.66	94.15	—	43.04
	7	86.67	83.90	87.84	—	91.64	93.37	—	28.11
	8	—	84.43	87.55	—	90.22	92.49	—	35.08
	10	—	81.84	86.43	—	90.08	92.38	—	66.06
	Mean ± σ	89.54 ± 2.77	86.36 ± 3.22	88.51 ± 1.76		92.40 ± 1.97	93.61 ± 1.25		

zooplankton food (Table 1) was measured gravimetrically, but it was not possible to obtain an accurate measurement of chitin in the feces because of their very high ash content. However, if it is assumed that chitin (39.37% C and 5.88% N by weight) was not assimilated by Atlantic menhaden, and the chitin C and N are then subtracted from the total C and N in the food and the feces, the calculated assimilation efficiency for zooplankton would be increased slightly, to 91.43% (C) and 93.99% (N) (Table 4, columns 6, 9).

Changes in assimilation efficiency within experiments followed the general trend of the elimination of feces (Figures 2, 3). During feeding, assimilation efficiency increased from initial low values to a peak, which was sustained for several hours after the end of feeding and thereafter declined. The peak assimilation was reached sooner, and remained elevated for longer, in the high ration experiments (Figures 2, 3). With the two smallest rations, assimilation was still ascending when the feeding period was terminated.

Assimilation remained high as long as the fecal elimination rate exceeded about 0.3 mg/g dry weight per h (Figure 5). At lower elimination rates, assimilation declined precipitously. The reduced assimilation efficiencies at the beginning and near the end of feces production were associated with the presence of a mucuslike material which the fish released with the feces when the elimination rate was low. This material resulted in high C:Si and N:Si ratios in these feces. Any such input of C and N to the feces other than from the food would reduce the calculated assimilation efficiency. With the smaller meal sizes a greater proportion of the feces were eliminated at a low rate (Table 4, column 10), and the materials produced by the digestive tract of the fish constituted a significant fraction of the total fecal material. This reduced the apparent overall assimilation efficiency (Table 4, columns 3, 4, 7). If the feces produced at low rates (<0.3 mg/g dry weight per h) are excluded from the calculation, the dependence of assimilation efficiency on ration size is reduced (Table 4, columns 5, 8).

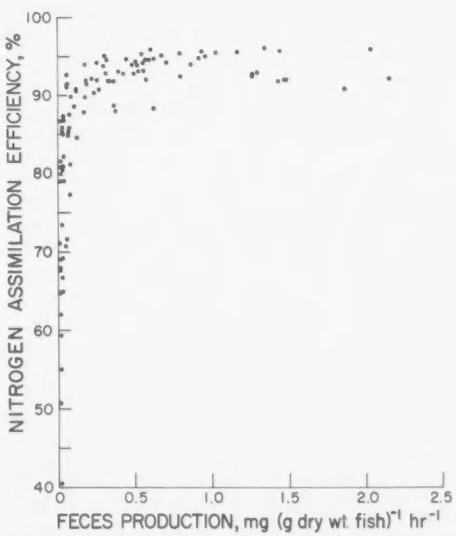

FIGURE 5.—Relationship between fecal elimination rate of *Brevoortia tyrannus* and the assimilation efficiency for nitrogen.

Nitrogen Excretion

When the fish were not feeding, their excretion rates were low and changes in the concentration of ammonia and DON in the tank were small. However, during feeding the excretion of the fish increased rapidly, and produced a rapid and nearly linear increase in the ammonia and DON concentrations (Figure 6). Excretion declined soon after the fish stopped feeding (Figure 7).

The mean ratio between DON and NH_3 excreted during the feeding period in all experiments was:

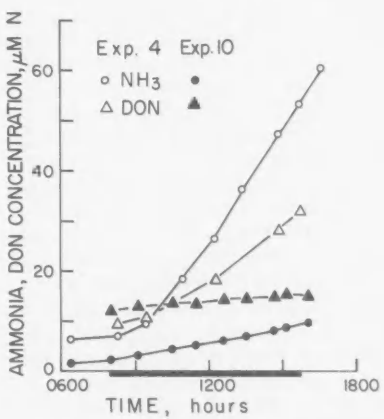

FIGURE 6.—Changes in ammonia and dissolved organic nitrogen concentration in the tank water due to excretion by 12 *Brevoortia tyrannus* during and after feeding. A high ration (Exp. 4) and a low ration (Exp. 10) experiment are illustrated.

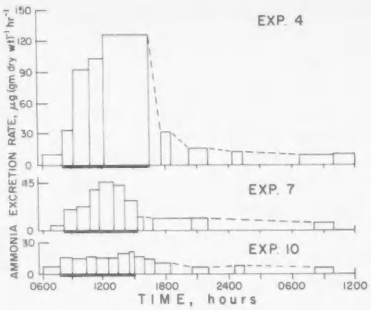

FIGURE 7.—Ammonia excretion rates of *Brevoortia tyrannus* before, during, and after a 7-h period of feeding on three ration sizes of *Ditylum brightwelli*.

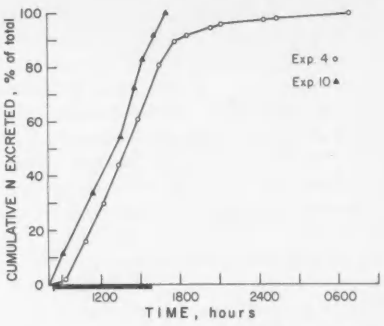

FIGURE 8.—Cumulative total exogenous nitrogen excreted by 12 *Brevoortia tyrannus* during and after feeding on *Ditylum brightwelli*. A high ration (Exp. 4) and a low ration (Exp. 10) experiment are illustrated.

$$\bar{X}\,\frac{\text{DON}-\text{N}}{\text{NH}_3-\text{N}} = 0.437, \quad \sigma = 0.088. \qquad (2)$$

Thus 30.4% of the total N excretion was in the form of DON, and 69.6% was in the form of ammonia.

The mean ±95% confidence limits of the ammonia excretion rate of fish unfed for 36 h (corresponding to measurement no. 1 in Durbin et al. 1981) was 7.46±2.54 μg NH_3-N/g dry weight per h. Using Equation (2), the total excretion was calculated to be 10.72±3.65 μg total N/g dry weight per h.

The amount of exogenous N excretion (that derived from the food) was calculated by subtracting the basal N excretion (10.72 μg N/g dry weight per h) from the total during the period of elevated excretion. Excretion rates were considered to have returned to basal when they reached the upper 95% confidence limit on the mean prefeeding rate, 14.4 μg N/g dry weight per h. Assimilation and N excretion did not lag far behind ingestion of the food. The time required for 50% of the exogenous N excretion to occur was only 1 or 2 h after 50% of the food was ingested ($\bar{X}$ = 1.4 h, Figure 8; Table 3, column 4). This indicates that all of the N ingested during the first 5.6 h of feeding (80% of the total) was assimilated during the feeding period.

The immediate decline in excretion rate after the fish stopped feeding was in accord with the decline in the elimination rate. In spite of this decline, 90% of the total exogenous excretion was completed within a mean of 2.4 h after the end of feeding (Figure 8; Table 3, column 6). The digestion and assimilation of *D. brightwelli* is therefore much more rapid than its complete elimination from the gut (i.e., compare Table 3, columns 4, 6 with columns 3, 5).

The total exogenous N excreted (E_N, milligrams/gram dry weight) increased linearly with both the total N ingested in the ration (R_N, milligrams) (Figure 9) and the N assimilated from the ration (pR_N, milligrams). The least squares linear regressions were:

$$E_N = 0.616R_N - 0.020 \qquad (3)$$
$$r = 0.99$$

$$E_N = 0.655pR_N - 0.016 \qquad (4)$$
$$r = 0.99$$

where p is the assimilation efficiency for N. These regressions indicate that approximately 61.6% of

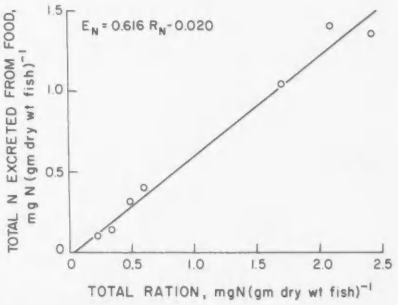

FIGURE 9.—Total exogenous nitrogen excreted by *Brevoortia tyrannus*, as a function of the amount of nitrogen ingested from *Ditylum brightwelli*. The least squares linear regression is shown.

the N in the ingested ration, and 65.5% of the N in the assimilated ration, were excreted.

If the total basal N excreted per day (0.257 mg N/g dry weight per d) is incorporated into Equations (3) and (4), the relationship between the total N excreted per day and the ingested N ration becomes:

$$E_N = 0.616R_N + 0.237 \text{ mg N/g dry weight per d} \quad (5)$$
$$r = 0.99$$

and the relationship between total daily N excretion and the assimilated N ration becomes (Figure 10):

$$E_N = 0.655pR_N + 0.241 \text{ mg N/g dry weight per d} \quad (6)$$
$$r = 0.99.$$

Equation (6) can be used to calculate, on a daily basis, the efficiency with which Atlantic menhaden retain N for growth as a function of N in the ration. This is analagous to calculating the net growth efficiency K_2:

$$K_2 = \frac{G}{pR} \quad (7)$$

where G = growth, grams/day
p = assimilation efficiency
R = ration, grams/day.

In the present case, growth in N (G_N, milligrams N/gram dry weight per day) will be equal to the N in the assimilated ration (pR_N) minus the total amount of N excreted per day (E_N total):

$$G_N = pR_N - E_N \quad (8)$$

$$= pR_N - (0.655\,pR_N + 0.241) \text{ mg N/g dry weight per d} \quad (9)$$

$$= 0.345\,pR_N - 0.241 \text{ mg N/g dry weight per d} \quad (10)$$

and

$$K_2 = \frac{0.345\,pR_N - 0.241}{pR_N} \quad (11)$$

K_2 calculated from Equation (11) for different assimilated ration sizes is shown in Figure 11. At an assimilated ration of 0.70 mg N/g dry weight per d there would be no net gain or loss of N. If Atlantic menhaden are composed of 8.03% N by weight (Table 1), this maintenance ration would correspond to 0.87% of their body N per day. The amount of N provided in the four lowest ration experiments was less than this daily maintenance requirement. The asymptotic value of K_2 at high ration levels was 0.345 (Figure 11). For K_2 = 0.20 and 0.30, the Atlantic menhaden would have to assimilate 1.66 and 5.36 mg N (2.1 and 6.7% of their body N, respectively) per day, with resultant growth rates of 0.42 and 2.01% of body N per day.

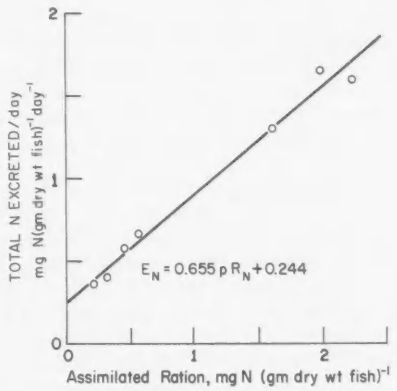

FIGURE 10.—Relationship between the amount of nitrogen assimilated from the daily ration, and the total daily nitrogen excretion by *Brevoortia tyrannus*.

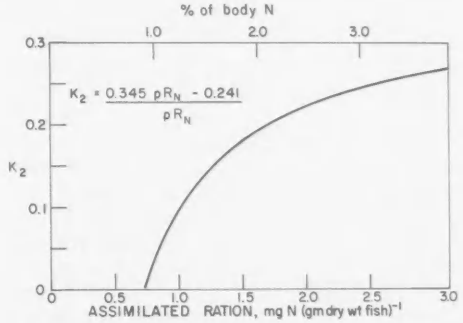

FIGURE 11.—Calculated efficiency of the utilization of nitrogen for growth by *Brevoortia tyrannus*, as a function of the nitrogen content of the assimilated ration.

Oxygen:Nitrogen Ratios

The ratio of O_2 consumed to N excreted (by atoms) has been used to give an indication of the type of food the fish are metabolizing. The O:N ratio during the combustion of protein is about 7.4 (Kutty 1972), while the ratio for carbohydrate is infinity, and for fat is about 415 (Ikeda 1977).

The change in the O:N ratio with time is shown for four phytoplankton experiments (Figure 12). The mean O:N for all initial prefeeding measurements in the phytoplankton experiments was 28.2, σ = 9.8. There was a slight increase of the O:N immediately after the beginning of feeding in most of the experiments. This was because the increase in the voluntary swimming speed of the fish during feeding produced an immediate increase in O_2 consumption, whereas N excretion increased more gradually. Swimming speeds and respiration rates during feeding in the three high ration experiments (nos. 4, 5, 6) averaged about 41.3 cm/s and 0.48 mg O_2/g wet weight per h, respectively. In these experiments, the O:N ratios declined to very low levels (between 5 and 10) soon after the initiation of feeding and remained at these low levels for the rest of the feeding period (Figure 12). In the four smaller ration experiments, the swimming speed during feeding ranged between 29.3 and 36.5 cm/s and O_2 consumption between 0.221 and 0.354 mg O_2/g wet weight per h.

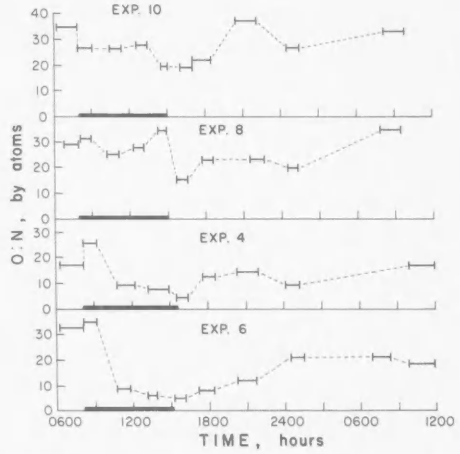

FIGURE 12.—O:N ratios of *Brevoortia tyrannus* before, during, and after feeding on *Ditylum brightwelli*. Oxygen data are from Durbin et al. (1981).

The decline in the O:N ratios during feeding was much less than in the high ration experiments. Swimming speeds and O_2 consumption rates of nonfeeding fish averaged about 12.2 cm/s and 0.10 mg O_2/g wet weight per h, respectively.

In all of the experiments, the lowest O:N ratio occurred immediately following feeding. This was because after the plankton was gone the fish immediately reduced their voluntary swimming speed and O_2 consumption, whereas their ammonia excretion remained high. Following this the O:N ratio gradually increased to the high prefeeding values.

DISCUSSION

Elimination of Food From the Gut

There has been some controversy concerning whether digestion rates and elimination rates are linear or exponential (Fänge and Grove 1979). In the linear model, a constant amount (g) is evacuated per unit time and therefore the instantaneous evacuation rate continually changes. In the exponential model, a constant proportion of the food present in the stomach is evacuated per unit time; thus, while the exponential rate remains constant, the actual amount of food (g) evacuated per unit time continually decreases.

In some studies the linear model has been explicitly used, by fitting a linear regression through the data points representing the food remaining in the stomach vs. time (e.g., Swenson and Smith 1973; Bagge 1977). In other studies the time to 100% evacuation of the stomach has been determined (e.g., Hunt 1960; Molnar and Tölg 1962; Edwards 1971; Jobling et al. 1977). Here there is usually an implicit assumption that evacuation is a linear process. Several recent careful studies, however, have found that gastric evacuation was clearly a curvilinear process which was closely approximated by an exponential curve (Brett and Higgs 1970; Tyler 1970; Elliott 1972; Elliott and Persson 1978). Beamish (1972) also concluded that evacuation is exponential over a major part of the digestion period, but that it may deviate at the beginning and near the end of digestion. In the initial stages this may occur if there is a lag between the ingestion of a meal, and the beginning of gastric evacuation. The final stages of evacuation are obviously not exponential, since completely empty stomachs are frequently seen in fishes.

With the Atlantic menhaden the exponential model seems appropriate since fecal elimination rates showed an exponential decline after the fish stopped feeding. This exponential fecal elimination rate (R'), determined from the decrease in fecal silicon elimination rate with time, is different from the exponential rate of gastric (stomach) evacuation (R), which is the factor measured in most studies. However, if the time required for food to travel the length of the intestine is constant, then the estimate of R' based on measurements of fecal elimination will be the same as R determined directly from measurements of the decline in stomach contents with time. In order to more fully investigate this, and to understand the patterns of change in feces elimination by Atlantic menhaden, especially during feeding, we have fit the data to a modified version of a model proposed by Elliott and Persson (1978). This theoretical model was then compared with our observed elimination rate data. A good agreement between the two would indicate that stomach evacuation is exponential, that R' is a good estimator of R, and that stomach evacuation is the principal factor governing the fecal elimination rate. Such an analysis may also serve to indicate whether systematic deviations between predicted and observed data occur as ration size changes.

The model of Elliott and Persson (1978) assumes that the fish feed at a constant rate, and that the gastric evacuation rate R is exponential. Thus the rate of change in stomach content (S) is given by:

$$(dS/dt) = F - RS. \tag{12}$$

The actual amount of food (S_t, milligrams/gram dry weight) present in the stomach after t hours is given by:

$$S_t = S_0 e^{-Rt} + \frac{F}{R}(1 - e^{-Rt}) \tag{13}$$

where S_0 is the initial amount of food in the stomach and F is the amount of food consumed per hour. As $F \to 0$, $S_t \to S_0 e^{-Rt}$. The amount of food (SE_t, milligrams/gram dry weight) which has been evacuated from the stomach by time t is simply:

$$SE_t = C_t - S_t \tag{14}$$

where C_t is the total amount of food (milligrams/gram dry weight) consumed in t hours. Thus SE_t and C_t are cumulative quantities measured since the onset of feeding, whereas S_t is the instantaneous amount present in the stomach at time t. For the present analysis we assumed that $R' = R$, and substituted R' into Equation (13). From values of R', F, and C_t for each experiment we then calculated S_t and SE_t for hourly intervals during and after feeding. All calculations were in terms of silicon, since this was not digested by the fish.

Curves illustrating C_t, S_t, and SE_t for the 12 fish are shown in Figure 13 for Experiment 7. The value of R' was 0.406/h and F was 0.241 mg Si/g dry weight per h. Since the ingestion rate was constant, C_t increased linearly with time. The amount of Si present in the stomach (S_t) increased curvilinearly during the feeding period, then declined exponentially after feeding stopped. The cumulative Si evacuated (SE_t) increased sigmoidally, with the inflection point at the time the fish stopped feeding. While most of the Si had been evacuated from the stomach within 5 h after the end of feeding, small amounts continued to be evacuated for many hours as the evacuation rates declined exponentially to very low levels.

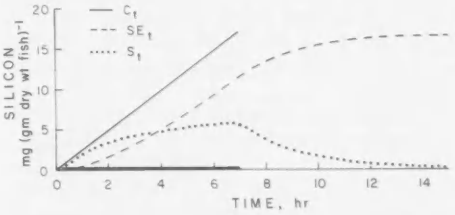

FIGURE 13.—Experiment 7. Cumulative ingestion of silicon (C_t), and model calculations of the instantaneous amounts of silicon present in the stomach (S_t) and the cumulative amounts of silicon which have been evacuated from the stomach (SE_t) during and after a 7-h feeding period.

The time lag between the ingestion of a particle and its elimination in the feces is the digestive tract residence time for that particle. Similarly the stomach residence time is the time lag between the ingestion and the gastric evacuation of a particle. The total digestive tract residence time was determined by subtracting the time required for the fish to ingest a given amount of Si, from the observed time when that same amount of Si was eliminated in the feces. The gastric residence time was similarly calculated from the observed feeding rate and the predicted values of SE_t. In each experiment the calculated gastric residence time followed a pattern similar to the digestive tract residence time (Figure 14). The two curves were

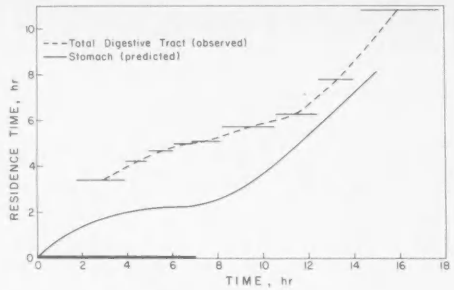

FIGURE 14.—Experiment 7. Changes in the digestive tract residence time of silicon (measured) and the stomach residence time of silicon (calculated) during and following a 7-h feeding period.

offset by the time required for Si to travel the length of the intestine; in the example shown, about 2 h.

Figure 14 demonstrates that particles eaten at the beginning of a feeding period have the shortest residence times. Residence time increases asymptotically during feeding, and then exponentially once the fish have stopped feeding. At the end of feeding the observed digestive tract residence time ranged between 5 and 6 h in all but the largest ration experiment, in which the residence time was only 4.5 h.

This model provides a quantitative explanation of the earlier observations by Noble (1973) and D. J. W. Moriarty and C. M. Moriarty (1973) that during continuous feeding, small food particles ingested early in the feeding period travel through the stomach more quickly than particles eaten later. In addition, observations that food particles eaten during continuous feeding will pass through the stomach more rapidly than when they are eaten as a single meal (i.e., Laurence 1971; Noble 1973) are also consistent with this model, since residence time remains short as long as feeding continues, but increases rapidly after the fish stop feeding.

Finally, the observed fecal elimination rates by the Atlantic menhaden (milligrams Si/gram dry weight per hour) were compared with the predicted gastric evacuation rates (milligrams Si/gram dry weight per hour) calculated from the model. Since the two curves were offset in time by the travel time of particles in the intestine, a comparison of the two is facilitated by lagging the stomach evacuation curve by the amount of the intestinal travel time. This time lag was graphically determined for each experiment by overlaying the curve of stomach evacuation on the curve of feces elimination rate such that the periods of exponential decline coincided. These lag times were quite similar for all experiments (overall mean $\pm\sigma$ = 2.17 $\pm$ 0.18 h). These values agree well with the average time for the first appearance of feces after the onset of feeding (2.4 h).

These plots of the observed fecal elimination rates and the predicted gastric evacuation rates (Figure 1) showed that in general there was good agreement between the two. There were, however, some systematic deviations with change in ration size. At high food rations, the observed elimination rates of the first fecal samples were higher than predicted by the model, indicating that these passed through the digestive tract more rapidly than predicted. In contrast, at the lowest rations the initial elimination rates were lower than predicted. Since the presence of food directly stimulates gastric motility and the secretion of digestive enzymes (Fänge and Grove 1979), it may be that the larger rations have a greater stimulatory effect on the digestive tract than small rations. It should be noted, however, that these deviations observed in the first two or three fecal samples represent food ingested quite early during the feeding period (Figure 1). Subsequent samples more closely followed the model.

The largest ration experiment (no. 6) also deviated from the model during the postfeeding period. The model predicts that if the exponential evacuation rate is <1 (i.e., in the present case = 0.366), food will continuously accumulate in the stomach during feeding (Figure 13). The largest amount of material in grams is therefore evacuated at the end of the feeding period (Figure 13), and the maximum fecal elimination rates should occur during the postfeeding period (because of the time required for material to travel through the intestine). However, in Experiment 6, the elimination rates quickly rose to high levels, but then declined and leveled off during the postfeeding period without reaching the maximum rates predicted by the model (Figure 1). This implies that stomach evacuation was also lower than the model would predict during the last 2 or 3 h of feeding. A possible explanation is that after the Atlantic menhaden had fed for several hours at this high rate, the amount of food may have accumulated in the stomach to an extent which exceeded the maximum physical capacity of the fish to process the material, which caused the gastric evacuation rate to level off. It was interesting that

assimilation efficiency in this experiment was also somewhat reduced. However, even with this high feeding rate, the behavior of the Atlantic menhaden did not change significantly during the course of the feeding period, and the fish gave no indication of approaching satiation (Durbin et al. 1981).

In summary we conclude that the calculated gastric evacuation by Atlantic menhaden calculated from Elliott and Persson's (1978) model agrees well with our experimental measurements of elimination rates following a meal. The calculated lag between the gastric evacuation of a particle and its elimination in the feces was similar for all ration sizes and also agreed well with the estimates of the time of the beginning of fecal elimination (Table 3, column 2). These results indicate that R' should be a good estimator of R. However, the stomach evacuation rates of Atlantic menhaden need to be determined directly, both in order to verify the model predictions, and to explore the reasons for the systematic deviations of the observed elimination from that predicted as food ration size changes.

Finally, with regard to methods employed for the study of fish digestion, present results with Atlantic menhaden indicate that when digestion is an exponential process, measurements of the time to "100% evacuation" are of limited value. This is because they cannot be used to determine the exponential evacuation rate R. The evacuation of the final portion of a meal is extremely protracted and may even be nonexponential. With Atlantic menhaden, for example, the food eliminated between 8 and 41 h after the end of feeding corresponded on average to the food ingested during the final 35 min of feeding; feces eliminated during hours 14-41 corresponded to the final 10 min of feeding. This makes selection of an end point, to be taken as 100%, quite difficult and arbitrary. If the final stages are nonexponential, then obviously the estimate of R would be biased. The final problem is computational: in an exponential process, the stage of 100% digestion is mathematically never reached, and it is necessary to approximate 100% with another value, such as 98, 99, or 99.9%. Although the choice of any of these values would be purely arbitrary, each provides a very different estimate of the value of R.

Assimilation Efficiency

The Atlantic menhaden was very efficient at absorbing N, C, and calories from both phytoplankton and zooplankton food. These high assimilation efficiencies are in general agreement with those reported for carnivorous fish (Gerking 1955; Menzel 1960; Pandian 1967; Beamish 1972; Kelso 1972). Few studies have examined the assimilation efficiency of herbivorous fishes. C. M. Moriarty and D. J. W. Moriarty (1973) and D. J. W. Moriarty and C. M. Moriarty (1973) found that the maximum mean C assimilation of *Tilapia nilotica* varied according to food type, being highest for the diatom *Nitzschia* (79%), somewhat lower for two bluegreen algae, *Microcystis* (70%) and *Anabaena* (75%), and least for the green alga *Chlorella* (49%). The average maximum C assimilation of *Haplochromis nigripinnis* for *Microcystis* was 71%. Menzel (1959) reported that *Holacanthus bermudensis* assimilated 85% (range 82-91%) of the N and 77.7% (range 72-84%) of the calories from two macroalgae, *Monostroma* and *Enteromorpha*. Plant materials described from the gut contents of Atlantic menhaden are planktonic and resuspended benthic diatoms, and detrital particles presumably derived from marsh grasses (Peck 1894; Darnell 1958; Peters and Kjelson 1975; Jeffries 1975). The high assimilation efficiency for *D. brightwelli* indicates that Atlantic menhaden should have high assimilation efficiency for other diatoms also. The ability of Atlantic menhaden to assimilate detrital material has not been experimentally determined. Planktonic green and bluegreen algae are much less important in the marine environment than in freshwater; moreover they are generally too small to be filtered by Atlantic menhaden (Durbin and Durbin 1975) and are not a significant food. Thus the comparatively low assimilation efficiency which has been reported for some freshwater herbivores fed green and bluegreen algae is not relevant to Atlantic menhaden or to most other marine phytoplankton-feeding fishes, which eat mainly diatoms and dinoflagellates (i.e., see Durbin 1979 and references therein).

Ration size has generally been shown to have little or no effect on assimilation efficiency (Gerking 1955; Pandian 1967; Beamish 1972; Kelso 1972; Solomon and Brafield 1972), although Elliott (1976) found that assimilation in brown trout, *Salmo trutta*, decreased as ration level increased.

Our results show a slight increase in assimilation efficiency with increasing meal size. This effect, as well as the changes in assimilation efficiency during the course of a feeding period, may have two possible causes: 1) the addition to the fecal pellets of significant quantities of materials

secreted by the gut, resulting in lower apparent assimilation efficiencies; and 2) a possible lag in the secretion of digestive enzymes after a period of fasting, which would cause assimilation to be initially low. The latter effect was observed by D. J. W. Moriarty and C. M. Moriarty (1973), who found that in *Tilapia* a period of about 4 h was required for the secretion of stomach enzymes, and hence assimilation efficiency, to reach high values. We have no measures of temporal changes in stomach enzymes for the Atlantic menhaden. While explanation 2 may have contributed to the initial low assimilation efficiency at the beginning of feeding, it would not explain the decline in assimilation towards the end of feces elimination, since this food was presumably digested at the end of the feeding period when stomach enzymes should have been maximal. Visual observations of the organic material surrounding the feces at low fecal production rates provided support for the first explanation, and would be consistent with the reduced assimilation efficiency observed at both the beginning and end of feces production.

The reason for the reduced assimilation efficiency at the highest ration level is unclear. If the maximum capacity of the digestive tract was reached, the assimilatory processes may have become saturated, causing a reduction in assimilation efficiency.

However, the supply rate of plankton in the highest ration experiment exceeded the concentration of diatoms which Atlantic menhaden would normally be expected to encounter on its summer feeding grounds in Narragansett Bay (Durbin and Durbin 1981). Thus Atlantic menhaden probably does not ordinarily feed at such high rates for prolonged periods in nature. Therefore, the slight decline in assimilation efficiency at the high feeding rate of Experiment 6 may not have much ecological significance. We conclude that overall, the effect of meal size on the assimilation efficiency of Atlantic menhaden is small. Because of the very rapid digestion rates and high assimilation efficiencies of Atlantic menhaden, this planktivore appears to be adapted to process efficiently large amounts of food continuously.

Nitrogen Excretion

In most teleosts ammonia is the principal end product of protein catabolism, and is the major component of N excretion; other N compounds excreted include urea, creatine, creatinine, and trimethylamine oxide (Watts and Watts 1974). In Atlantic menhaden the percent of total N excreted as ammonia (69.6%) appears to be similar to that observed in other species (Smith 1929; Atherton and Aitken 1970; McCarthy and Whitledge 1972).

Nitrogen excretion by Atlantic menhaden changed according to whether or not the fish were feeding, the rate at which they fed, and the time since the last meal. Previous studies have also found that N excretion increases as a result of feeding (Brett and Zala 1975; Elliott 1976; Savitz et al. 1977). These studies differed from the present study, however, in the timing of the peak of N excretion and the subsequent return to endogenous rates. Fingerling sockeye salmon, *Oncorhynchus nerka*, at 15° C showed a peak ammonia excretion rate about 4 h after a meal and did not return to a basal rate until about 16 h after feeding (Brett and Zala 1975). Similarly, N excretion rates of brown trout at 17° C did not return to baseline until about 12-20 h after feeding (Elliott 1976) and largemouth bass, *Micropterus salmoides*, at 21°-23° C took 1 or 2 d (Savitz et al. 1977). In contrast, when Atlantic menhaden fed continuously for 7 h, the excretion rate remained high throughout the feeding period and lagged only 1 or 2 h behind ingestion of the food. The return to baseline was also rapid, with 90% of the exogenous N excretion occurring within a mean of 2.4 h following the end of feeding.

The Atlantic menhaden excreted a constant proportion of N in its ration (61.6% of the ingested and 65.5% of the assimilated ration). Savitz et al. (1977) also found a linear relationship between ingestion and N excretion in largemouth bass, although in that case only 40% of the ingested N was excreted. Gerking (1971) reported that in bluegill there was a linear relationship between the amount of N consumed and the amount retained for growth, which implied that the relationship between the amount of N ingested and that excreted was also linear. Additional studies are needed to determine the extent to which the proportion of N excreted by different species varies. Factors which may be expected to affect this proportion are the nutritional requirements of the fish, which may change seasonally, relative to the chemical composition of the food.

Oxygen:Nitrogen Ratios

The chemical composition of Atlantic menhaden compared with that of plankton indicates that the

fish conserve C and calories relative to N and ash from its food. Exogenous N in excess of body requirements is excreted. The O:N ratios indicate that proteins are used as a metabolic fuel by both feeding and nonfeeding Atlantic menhaden with subsequent excretion of N. This is consistent with results from other teleosts (Watts and Watts 1974). If an O:N ratio of 7.4 indicates that pure protein is being burned, then the mean value of 28.2 in fish unfed for 36 h indicates that 7.4/28.2 = 26.2% of the O_2 consumed is being used for protein catabolism. The increase in O:N ratios immediately after the beginning of feeding indicates that the fish are metabolizing proportionally more carbohydrate or lipid to support the increased swimming speed until significant quantities of food have been assimilated and become available as an energy source. During the feeding period of the three high ration experiments, the O:N ratios declined to or below that associated with the combustion of pure protein. The decline in the O:N ratios during feeding can be caused by two processes, which can act simultaneously: the fish are obtaining a large proportion of their energy directly from the breakdown of the C skeletons of amino acids absorbed from the food, with subsequent excretion of the N; and the proportions of the various amino acids taken in the food are being balanced to meet the requirements of protein synthesis; excess α-amino acids are excreted (Watts and Watts 1974). While it is impossible to separate the two processes in the present experiments, O:N ratios below 7.4 are an indication that both are occurring.

Kutty (1978) has calculated the ammonia quotient (AQ = NH_3 excreted/O_2 consumed) from the data of Brett and Zala (1975), from which O:N ratios can be determined. In that study the fish were fed a single meal over a brief time interval, and the peaks in O_2 consumption and N excretion were separated by several hours. However, the trend in the O:N ratios was similar to the present study, in that they declined from high values ($\approx$ 40.0) in the unfed fish to a minimum of about 8.3 during the digestion and assimilation of the food, then gradually increased to the prefeeding level.

ACKNOWLEDGMENT

We would like to thank Harold Loftes, skipper of the *Ocean State*, and Charles Follett, skipper of the *Cindy Bett*, for their assistance in obtaining Atlantic menhaden. We also thank Theodore Smayda for the use of his laboratory facilities, Thomas Smayda and Peter Verity for their assistance during the experiments, and the National Science Foundation for support of this research under grant OCE 7602572.

LITERATURE CITED

ATHERTON, W. D., AND A. AITKEN.
1970. Growth, nitrogen metabolism and fat metabolism in *Salmo gairdneri*, Rich. Comp. Biochem. Physiol. 36:719-747.

BAGGE, O.
1977. Meal size and digestion in cod (*Gadus morrhua* L.) and sea scorpion (*Myoxocephalus scorpius* L.). Medd. Dan. Fish. Havunders. N.S. 7:437-446.

BEAMISH, F. W. H.
1972. Ration size and digestion in largemouth bass, *Micropterus salmoides* Lacépède. Can. J. Zool. 50:153-164.

BRETT, J. R., AND D. A. HIGGS.
1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka*. J. Fish. Res. Board Can. 27:1767-1779.

BRETT, J. R., AND C. A. ZALA.
1975. Daily pattern of nitrogen excretion and oxygen consumption of sockeye salmon (*Oncorhynchus nerka*) under controlled conditions. J. Fish. Res. Board Can. 32:2479-2486.

DARNELL, R. M.
1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publ. Inst. Mar. Sci. Univ. Tex. 5:353-416.

D'ELIA, C. F., P. A. STEUDLER, AND N. CORWIN.
1977. Determination of total nitrogen in aqueous samples using persulfate digestion. Limnol. Oceanogr. 22:760-764.

DURBIN, A. G.
1979. Food selection by plankton feeding fishes. *In* H. Clepper (editor), Predator-prey systems in fisheries management, p. 203-218. Sport Fish. Inst., Wash., D.C.

DURBIN, A. G., AND E. G. DURBIN.
1975. Grazing rates of the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration. Mar. Biol. (Berl.) 33:265-277.
1981. Standing stock and estimated production rates of phytoplankton and zooplankton in Narragansett Bay, Rhode Island. Estuaries 4:24-41.

DURBIN, A. G., E. G. DURBIN, P. G. VERITY, AND T. J. SMAYDA.
1981. Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the Atlantic menhaden *Brevoortia tyrannus* (Pisces: Clupeidae). Fish. Bull., U.S. 78:877-886.

DURBIN, E. G.
1977. Studies on the autecology of the marine diatom *Thalassiosira nordenskioeldii*. II. The influence of cell size on growth rate, and carbon, nitrogen, chlorophyll *a* and silica content. J. Phycol. 13:150-155.

EDWARDS, D. J.
1971. Effect of temperature on rate of passage of food through the alimentary canal of the plaice *Pleuronectes platessa* L. J. Fish Biol. 3:433-439.

ELLIOTT, J. M.
1972. Rates of gastric evacuation in brown trout, *Salmo trutta* L. Freshwater Biol. 2:1-18.
1976. Energy losses in the waste products of brown trout (*Salmo trutta* L.). J. Anim. Ecol. 45:561-580.

ELLIOTT, J. M., AND L. PERSSON.
1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977-991.

FÄNGE, R., AND D. GROVE.
1979. Digestion. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology, Vol. VIII, p. 161-260. Acad. Press, N.Y.

GERKING, S. D.
1955. Influence of rate of feeding on body composition and protein metabolism of bluegill sunfish. Physiol. Zool. 28:267-282.
1971. Influence of rate of feeding and body weight on protein metabolism of bluegill sunfish. Physiol. Zool. 44:9-19.

HUNT, B. P.
1960. Digestion rate and food consumption of Florida gar, warmouth, and largemouth bass. Trans. Am. Fish. Soc. 89:206-211.

IKEDA, T.
1977. The effect of laboratory conditions on the extrapolation of experimental measurements to the ecology of marine zooplankton. IV. Changes in respiration and excretion rates of boreal zooplankton species maintained under fed and starved conditions. Mar. Biol. (Berl.) 41:241-252.

JEFFRIES, H. P.
1975. Diets of juvenile menhaden (*Brevoortia tyrannus*) in three estuarine habitats as determined from fatty acid composition of gut contents. J. Fish. Res. Board Can. 32:587-592.

JOBLING, M., D. GWYTHER, AND D. J. GROVE.
1977. Some effects of temperature, meal size and body weight on gastric evacuation time in the dab *Limanda limanda* (L). J. Fish Biol. 10:291-298.

KELSO, J. R. M.
1972. Conversion, maintenance, and assimilation for walleye, *Stizostedion vitreum vitreum*, as affected by size, diet, and temperature. J. Fish. Res. Board Can. 29:1181-1192.

KUTTY, M. N.
1972. Respiratory quotient and ammonia excretion in *Tilapia mossambica*. Mar. Biol. (Berl.) 16:126-133.
1978. Ammonia quotient in sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 35:1003-1005.

LAURENCE, G. C.
1971. Feeding and bioenergetics of largemouth bass larvae (*Micropterus salmoides*). Ph.D. Thesis, Cornell Univ., Ithaca, 139 p.

MCCARTHY, J. J., AND T. E. WHITLEDGE.
1972. Nitrogen excretion by anchovy (*Engraulis mordax* and *E. ringens*) and jack mackerel (*Trachurus symmetricus*). Fish. Bull., U.S. 70:395-401.

MENZEL, D. W.
1959. Utilization of algae for growth by the angelfish, *Holacanthus bermudensis*. J. Cons. 24:308-313.
1960. Utilization of food by a Bermuda reef fish, *Epinephelus guttatus*. J. Cons. 25:216-222.

MOLNÁR, G., AND I. TÖLG.
1962. Relation between water temperature and gastric digestion of largemouth bass (*Micropterus salmoides* Lacépède). J. Fish. Res. Board Can. 19:1005-1012.

MORIARTY, C. M., AND D. J. W. MORIARTY.
1973. Quantitative estimation of the daily ingestion of phytoplankton by *Tilapia nilotica* and *Haplochromis nigripinnis* in Lake George, Uganda. J. Zool. (Lond.) 171:15-23.

MORIARTY, D. J. W., AND C. M. MORIARTY.
1973. The assimilation of carbon from phytoplankton by two herbivorous fishes: *Tilapia nilotica* and *Haplochromis nigripinnis*. J. Zool. (Lond.) 171:41-55.

NOBLE, R. L.
1973. Evacuation rates of young yellow perch, *Perca flavescens* (Mitchill). Trans. Am. Fish. Soc. 102:759-763.

PANDIAN, T. J.
1967. Intake, digestion, absorption and conversion of food in the fishes *Megalops cyprinoides* and *Ophiocephalus striatus*. Mar. Biol. (Berl.) 1:16-32.

PECK, J. I.
1894. On the food of the menhaden. Bull. U.S. Fish. Comm. 13:113-126.

PETERS, D. S., AND M. A. KJELSON.
1975. Consumption and utilization of food by various postlarval and juvenile fishes of North Carolina estuaries. *In* L. E. Cronin (editor), Estuarine research, Vol. I, p. 448-472. Acad. Press, N.Y.

SAVITZ, J., E. ALBANESE, M. J. EVINGER, AND P. KOLASINSKI.
1977. Effect of ration level on nitrogen excretion, nitrogen retention and efficiency of nitrogen utilization for growth in largemouth bass (*Micropterus salmoides*). J. Fish Biol. 11:185-192.

SMITH, H. W.
1929. The excretion of ammonia and urea by the gills of fish. J. Biol. Chem. 81:727-742.

SOLOMON, D. J., AND A. E. BRAFIELD.
1972. The energetics of feeding, metabolism and growth of perch (*Perca fluviatilis* L.). J. Anim. Ecol. 41:699-718.

SOLÓRZANO, L.
1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. 14:799-801.

STRICKLAND, J. D. H., AND T. R. PARSONS.
1972. A practical handbook of seawater analysis. 2d ed. Fish. Res. Board Can., Bull. 167, 310 p.

SWENSON, W. A., AND L. L. SMITH, JR.
1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 30:1327-1336.

TYLER, A. V.
1970. Rates of gastric emptying in young cod. J. Fish. Res. Board Can. 27:1177-1189.

WATTS, R. L., AND D. C. WATTS.
1974. Nitrogen metabolism in fishes. *In* M. Florkin and B. Scheer (editors), Chemical zoology, Vol. VIII, p. 369-446. Acad. Press, N.Y.

WINDELL, J. T.
1966. Rate of digestion in the bluegill sunfish. Invest. Indiana Lakes Streams 7:185-214.

TAXONOMIC STATUS AND BIOLOGY OF THE BIGEYE THRESHER, *ALOPIAS SUPERCILIOSUS*

S. H. GRUBER[1] AND L. J. V. COMPAGNO[2]

ABSTRACT

This paper reviews the life history, taxonomic status, abundance, distribution and habitat, reproduction, feeding habits, scientific and economic importance, and literature of the bigeye thresher, *Alopias superciliosus*; and presents new information on morphometrics, vertebral counts, tooth counts, denticles, size, age, and growth from 22 specimens. We found *A. profundus* is a junior synonym of *A. superciliosus*, and we have extended the geographic range of the latter to the Mediterranean Sea and New Zealand. *Alopias superciliosus* is a wide-ranging, circumtropical species between the latitudinal limits of 40° north and 40° south.

Thresher sharks (family Alopiidae, genus *Alopias*), instantly recognizable by their tremendously elongated caudal fins (the upper lobe of the caudal fin about as long as the rest of the shark), have been known since antiquity. According to Salviani (1554), Aristotle was familiar with thresher sharks and described their behavior. Bonnaterre (1788) proposed the first valid specific name for a thresher, *Squalus vulpinus* (the common thresher), while Rafinesque (1809) proposed the genus *Alopias* for the same species, which he termed *Alopias macrourus*. More recently Tortonese (1938), Bigelow and Schroeder (1948), and Bass et al. (1975) reviewed the systematics of the genus *Alopias*.

Lowe (1839) described new fishes from Madeira in the eastern Atlantic. Among these was a very brief diagnosis of a new thresher, *Alopecias superciliosus*, which he characterized as follows: "At once distinguished from the only other known species of the genus, *Carcharias vulpes*, Cuv., by the enormous eye and its prominent brow. I have at present only seen a single young example."

This shark, the bigeye thresher, was not mentioned by name in the literature until Fowler (1936) erroneously synonymized it with *Alopias vulpinus* (Bonnaterre 1788). The species was apparently overlooked in the reviews of Dumeril (1865), Günther (1870), Garman (1913), White (1937), and Tortonese (1938). Bigelow and Schroeder (1948) resurrected Lowe's species and gave the first detailed diagnosis and description of *Alopias superciliosus*, based on Floridian and Cuban specimens. Earlier, Grey (1928), Nakamura (1935), and Springer (1943) reported specimens of the bigeye thresher under different scientific names, but all of these writers overlooked Lowe's obscure account. More recently, Cadenat (1956), Strasburg (1958), Fitch and Craig (1964), Kato et al. (1967), Telles (1970), Bass et al. (1975), and Stillwell and Casey (1976) have presented descriptive accounts as well as morphometric, meristic, and other quantitative data on the species.

Thresher sharks are peculiar in that their elongated tails are the only known structure in sharks, other than jaws and teeth and the armed rostrum of sawsharks (Pristiophoridae), that function in killing or immobilizing prey (Springer 1961). An Indo-Pacific orectoloboid, the zebra shark, *Stegostoma fasciatum* (family Stegostomatidae), also has a greatly elongated caudal fin, but is not known to use it as a weapon.

Bigeye threshers are noteworthy in having enormous, dorsally facing eyes and unique head grooves, structures which may reflect specialized habits of the species that differ from the other two species of thresher shark.

The impression gained in most of the taxonomic literature is that *A. superciliosus* is a widespread but rare species. However, the works of Gubanov (1972), Guitart Manday (1975), and Stillwell and Casey (1976) indicate that it can be locally abundant and of importance in pelagic longline fisheries of the west-central Atlantic and northwestern Indian Ocean.

[1]Biology and Living Resources, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149.
[2]Tiburon Center for Environmental Studies, San Francisco State University, Tiburon, CA 94920.

Manuscript accepted June 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

The purpose of this paper is to bring together the widely scattered information on *A. superciliosus*, summarize its life history, and correct certain inconsistencies in the literature. We present morphometric, meristic, and other quantitative data, including descriptive accounts of specimens from Florida and the central Pacific, compare the bigeye thresher with other species of threshers, and discuss its taxonomic history.

MATERIAL

1. SHG-A2 (S. H. Gruber, private collection); adult female, 356 cm TL (total length), weight 140 kg; Straits of Florida several kilometers east of Miami Beach, Fla.; captured on 29 June 1977 by sport fishermen on a hook baited with squid at 30 m depth in water about 400 m deep. The specimen was photographed, measured, and dissected, and two early fetuses, both eyes, skin patch, and the tail were saved. The jaws were used in a taxidermist's mount and were not available, but the teeth were photographed before the fish was mounted. The fetuses are males, 207 and 213 mm TL.

2. SHG-A7; adult male, 356 cm TL; Straits of Florida several kilometers east of Pompano Beach, Fla.; captured at 1000 h e.d.t. on 4 July 1979 by commercial longliner at 40 m in water about 400 m deep. The specimen was photographed, measured, and dissected. Head, jaws, vertebral column (precaudal), tail, and claspers were saved. The spiral valve was sent to M. Dailey, Long Beach, Calif., for parasite investigation. One eye was sent to G. Hughes, Canberra City, Australia, for retinal study.

3. SHG-A5; adult female, 320 cm TL; Straits of Florida several kilometers east of Miami Beach, Fla.; captured on a longline at 40 m at 2200 h e.s.t., 14 March 1979. The water depth was 350 m. The head was removed, dissected, and saved with the jaws intact.

4. SHG-A6; subadult female, 306 cm TL; caught on same set as no. 3 above.

5. SHG-A3; subadult male, 291 cm TL; Straits of Florida, 35 km east of Palm Beach, Fla.; captured on 24 July 1979 by commercial longliner at 30 m in water about 120 m deep. The specimen was photographed, measured, and dissected, and the jaws, vertebrae, and head saved.

6. SHG-A4; immature male, 150 cm TL; east of Hatteras, N.C.; captured on a longline on 6 May 1979. The specimen was photographed and measured. No parts were saved as the whole shark was used in taxidermy.

7. *Shoyo Maru* voyage 13, SM-9-II-64-3; Nankai Regional Fisheries Laboratory, Japan; immature female, 279 cm TL, weight 62 kg; eastern Central Pacific, lat. 0°38′ N, long. 124°23′ W; captured on a longline on 9 February 1964. The specimen was photographed, measured, and dissected by Susumu Kato[3]; skin, jaws, reproductive organs, eyes, nasal sac, and parasites saved.

8. LJVC-0355 (L. J. V. Compagno, private collection), *Shoyo Maru* voyage 13, SM-11-II-6493; immature female, 287 cm TL, weight 59 kg; eastern Central Pacific, lat. 3°16′ S, long. 128°18′W; captured on a longline on 11 February 1964. The specimen was measured and preserved intact by Susumu Kato (footnote 3), later photographed and dissected by Compagno; skin, jaws, cranium, eyes, vertebral column, and fins saved.

9. *Shoyo Maru* voyage 16, SHO-16-2; 461 cm TL; Mediterranean Sea, lat. 36°39′ N, long. 17°51′ E; captured on a longline on 2 December 1966. Specimen measured by Izumi Nakamura[4] and data presented to Susumu Kato (footnote 3).

10. *Shoyo Maru* voyage 16, SHO-16-22; 2 individuals, 343 and 347 cm TL; lat. 13°36.4′ N, long. 75°34.2′ W; captured on a longline on 4 February 1967. Specimen measured by Izumi Nakamura (footnote 4) and data presented to Susumu Kato (footnote 3).

11. LACM-F-89; no length or sex data; Odawara, Japan, 1968; jaws only, teeth counted by Bruce Welton[5].

12. CAS (California Academy of Science, San Francisco, Calif.) Acc. 1963-X: 7; adult male, 372 cm TL; off San Clemente Is., southern California, 23 July 1963; partly dissected and preserved, jaws dried; previously reported by Fitch and Craig (1964).

13. LACM-F-88; male, presumably adult, 378 cm TL; 25 km ESE of east end of Santa Catalina Is., Calif., 30 June 1967; jaws only, teeth counted by Bruce Welton (footnote 5).

14. LACM-F-90; immature female, ca. 305 cm TL; southern California, probably Santa Mon-

[3]Susumu Kato, Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

[4]Izumi Nakamura, Fisheries Research Station, Kyoto University, Maizuru, Kyoto 625, Japan.

[5]Bruce Welton, Department of Paleontology, Los Angeles Museum of Natural History, 900 Exposition Boulevard, Los Angeles, CA 90007.

ica Bay area, 26 October 1966; jaws only, teeth counted by Bruce Welton (footnote 5).

15. Several other examples are listed in the tables on tooth counts but were not otherwise measured or seen.

DISTINCTIVE CHARACTERS

Alopias superciliosus (Figures 1-4) can be immediately distinguished from other threshers by its unique head shape, with lateral grooves

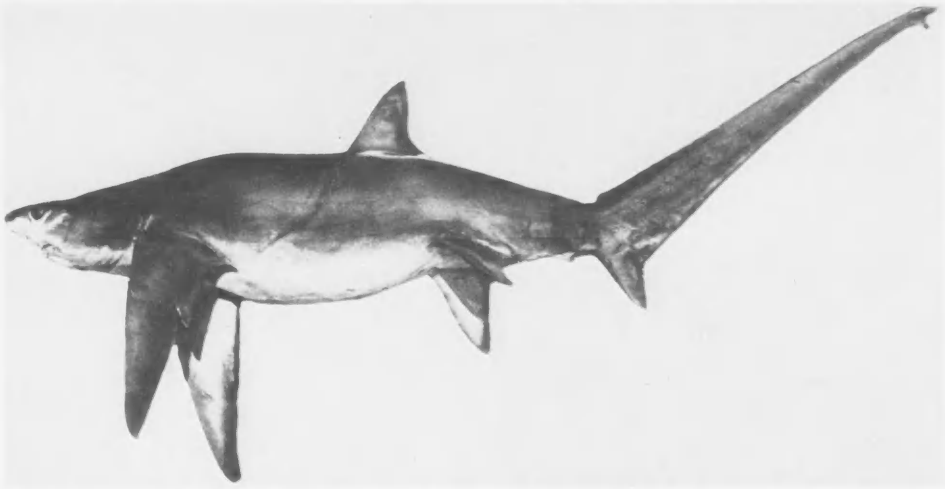

FIGURE 1.—Lateral view of a 356 cm TL, 140 kg female *Alopias superciliosus* (SHG-A2) taken off Miami Beach, Fla. Detailed measurements of this shark are given in Table 1, column 1. The characteristic head grooves are not clearly shown because of the slightly ventral angle of the photograph. Photo: S. Gruber.

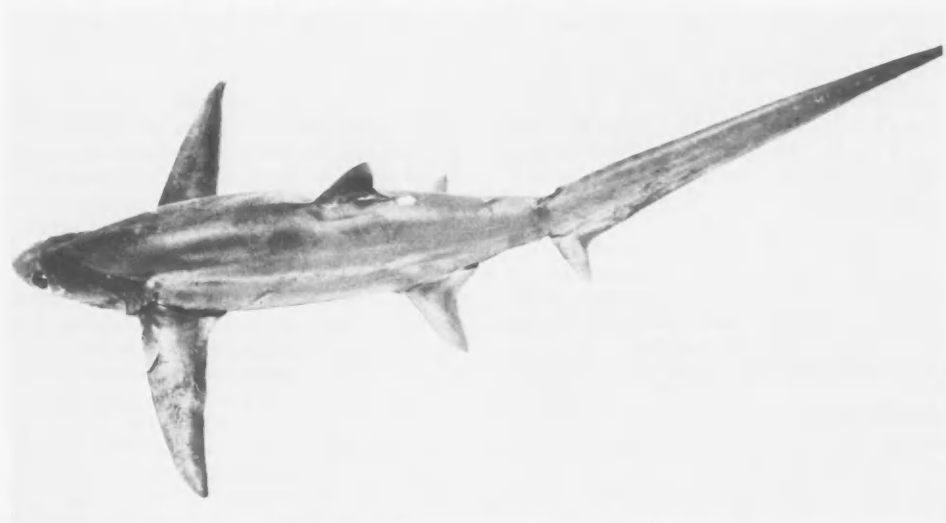

FIGURE 2.—Dorsal view of *Alopias superciliosus* (SHG-A2). The head grooves and upward-looking eyes are more easily seen in this photograph. Photo: S. Gruber.

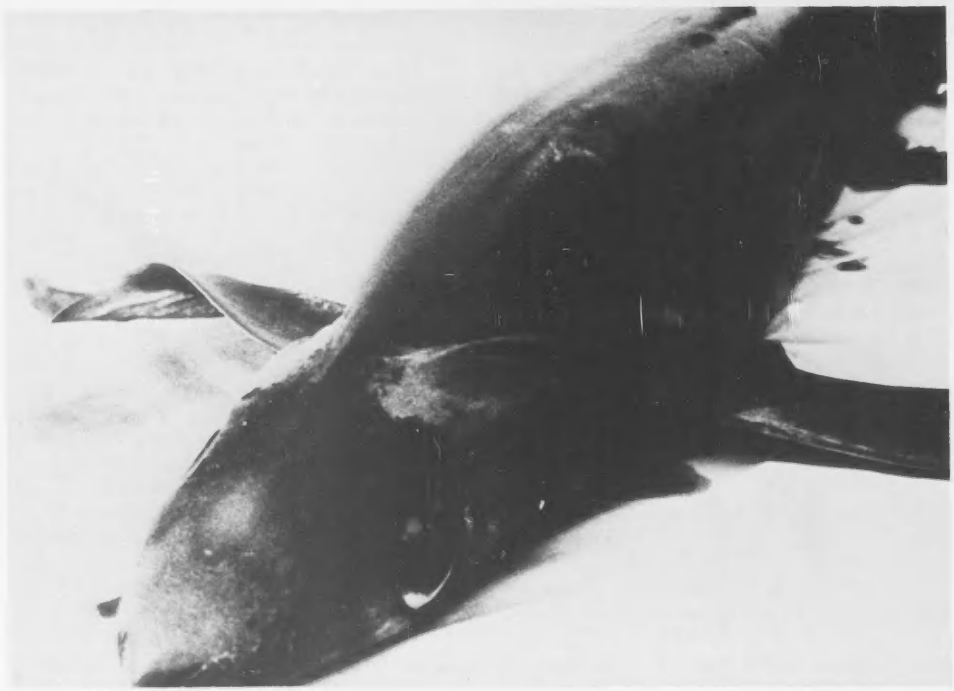

FIGURE 3.—Three-quarter lateral view of the head of a 159 cm TL immature male *Alopias superciliosus* (SHG-A4) showing the head grooves and massive "crest" composed of the epaxial musculature. The characteristic large eyes, bulbous snout and flattened interorbital space can also be seen. The crest and grooves are even more pronounced in mature bigeye threshers. Photo: S. Gruber.

above the branchial region, bulbous snout (more tapering in other threshers), nearly flat interorbital space (highly arched in other species), huge eyes with lids shaped like an inverted pear or keyhole (in individuals >1,300 mm TL) that extend onto the dorsal surface of the head (Figure 4), and a distinct indentation or step in the profile of the forehead at the origin of the head grooves that gives the head a helmeted or crested appearance (other thresher species have the forehead convex or flat but not indented; the indentation is less marked in fetal bigeye threshers). In addition, the bigeye thresher has much larger and less numerous teeth than other threshers, e.g., 24/24 rows or less (32/29 or more in other species). Tooth row groups represented in the adult dentition of the bigeye thresher include anterior and lateroposterior teeth only, without the symphysial or intermediate teeth found in other species. The bigeye thresher has fewer vertebrae, 278-308, than other threshers, which have 339-472 (Springer and Garrick 1964; Bass et al., 1975; unpublished data on all three species). In the monospondylous precaudal region of the vertebral column, the vertebral calcification patterns of the bigeye thresher are simpler than in other species, with fewer radii in the intermedialia and no fusion of their bases (extensively fused in *A. pelagicus*). The first dorsal fin of the bigeye thresher is positioned more posteriorly on the back than in other species of threshers, with the midpoint of its base much closer to the pelvic fin bases than to the pectoral bases, and with its free rear tip over or slightly anterior to the pelvic origins. In *A. pelagicus* and *A. vulpinus* the midpoint of the first dorsal base is usually closer to the pectoral fin bases than to the pelvic bases (occasionally equidistant between pectoral and pelvic bases), and the free rear tip of the first dorsal is far anterior to the pelvic origins.

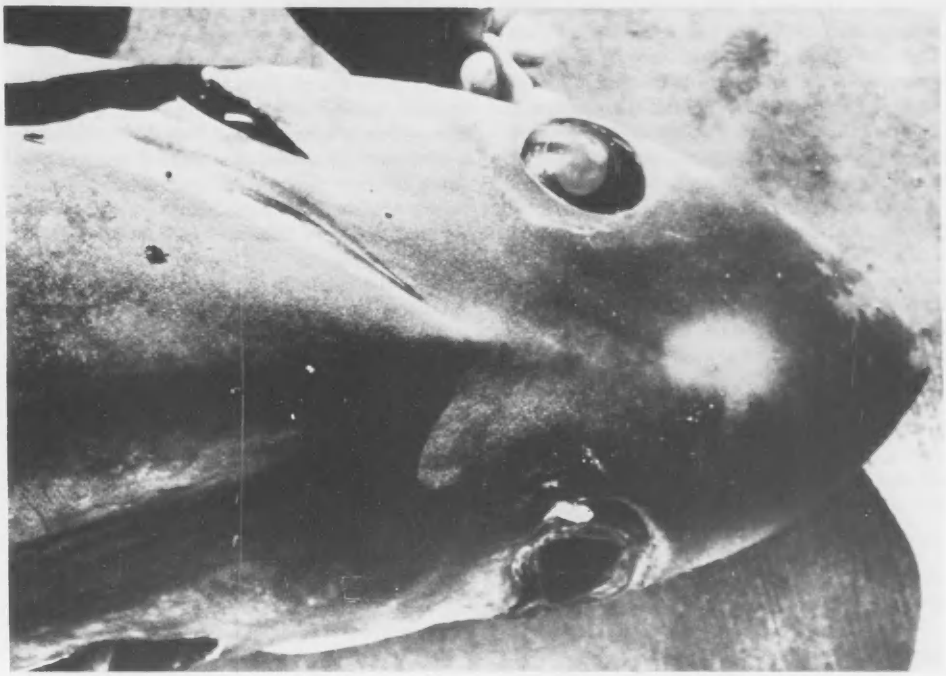

FIGURE 4.—Dorsal view of the head of a 356 cm TL male *Alopias superciliosus* (SHG-A7) showing the head grooves and upward looking eyes. (The lens of the right eye has been removed.) Photo: S. Spielman.

STATUS OF *ALOPIAS PROFUNDUS*

Nakamura (1935) described two new species of thresher sharks, *A. profundus* and *A. pelagicus*, from Taiwan. The thresher sharks were collected at a fish market and capture data were unavailable. Nakamura thought that one of these species lived near the sea bottom and so named it *A. profundus*. He was evidently unaware of Lowe's account of *A. superciliosus*, and only compared his new species with each other. Nakamura concluded that there was insufficient evidence in the literature to determine if either of his two species was equivalent to the wide-ranging "*Alopias vulpes*" (= *A. vulpinus*), and gave this reason as justification in naming *A. profundus* and *A. pelagicus*.

Fowler (1941) listed both Nakamura's species as questionable synonyms of *A. vulpinus* but Bigelow and Schroeder (1948) recognized them as distinct. They noted that *Alopias* can be divided into two groups, one including *A. profundus* and *A. superciliosus*, both with the free rear tip of the first dorsal fin extending to over the pelvic origins and with huge eyes; and the other including *A. vulpinus*, *A. pelagicus*, and the dubious *A. caudatus*, having the first dorsal rear tip well anterior to the pelvic origins and with smaller eyes. Using Nakamura's (1935) account as a source for *A. profundus*, Bigelow and Schroeder (1948) distinguished the two species in the "bigeye" group as follows:

1) "Rear tip of 2nd dorsal terminates considerably anterior to origin of anal; pelvics a little higher vertically than 1st dorsal and a little larger in area; anterior margin of 1st dorsal strongly convex; no lower precaudal pit." *Alopias superciliosus*.

2) "Rear tip of 2nd dorsal terminating over base of anal; pelvics less than 1/2 as high vertically as 1st dorsal and much smaller in area; anterior margin of 1st dorsal only very weakly convex; a precaudal pit below as well as above." *Alopias profundus*.

Several writers, following Bigelow and Schroed-

er (1948), including Teng (1962), Matsubara (1963), Chen (1963), Garrick and Schultz (1963), Fitch and Craig (1964), and Kato et al. (1967), recognized *A. profundus* as distinct, though Kato et al. suggested that it might be identical to *A. superciliosus*. Bass et al. (1975) synonymized *A. profundus* and *A. superciliosus* because the relative positions of anal and second dorsal fins, relative sizes of first dorsal and pelvic fins, and absence of a lower precaudal pit were, in their opinion, "...highly variable and probably invalid as diagnostic characters," but they did not discuss the matter further. Our analysis of the characters supposedly separating *A. profundus* and *A. superciliosus* leads us to concur with Bass et al. in synonymizing these species.

We have taken Nakamura's (1935) original measurements of *A. profundus* and converted them to precaudal proportions for comparison with other bigeye threshers (Table 1) and find that most of them fall within the range for other specimens identified as *A. superciliosus*. The differences listed by Bigelow and Schroeder (1948) for *A. profundus* and *A. superciliosus* appear to be based on ontogenetic changes and individual variation in a single species, or, in the case of the pelvic

TABLE 1.—Measurements of 13 specimens of *Alopias superciliosus* from the Atlantic, Indian, and Pacific Oceans. All values are proportional to precaudal length (given as unity) except rows 1 and 2 which are in centimeters as indicated.

Item	Original SG-A2 Western North Atlantic Female	Original SG-A7 Western North Atlantic Male	Stillwell and Casey (1975) Western North Atlantic Female	Original SG-A3 Western North Atlantic Male	Original SG-A4 Western North Atlantic Male	Bigelow and Schroeder (1948) Western North Atlantic Male	Telles (1975) Eastern North Atlantic Male	Bass et al. (1975) Western Indian Male	Nakamura (1935) Western North Pacific Female	Strasburg et al. (1958) Central North Pacific Male	Original SM-9-11-64-3 Eastern Central Pacific Female	Original LJVC 0355 Eastern Central Pacific Female	Fitch and Craig (1964) Eastern North Pacific Male
Total length, cm	356	356	340	290.8	159	130	269	363	332	328	279	287	381
Precaudal length, cm	201	199.4	190	150.4	84.5	66	152	198	170	167.4	139	144	208
Snout to													
Mouth	085	089	087	094	123	118	079	078	—	061	099	097	076
Eye	080	087	074	096	109	—	—	062	—	—	078	079	—
Pectoral origin	269	286	287	316	328	333	252	265	300	309	320	306	—
Pelvic origin	697	701	702	735	734	716	692	729	729	744	770	716	740
Anal origin	876	930	926	939	976	938	921	—	929	957	—	—	952
1st dorsal origin	535	586	569	603	621	612	562	557	588	595	612	597	600
2d dorsal origin	866	853	874	916	911	903	—	—	894	902	906	903	918
Internarial	027	028	029	031	034	035	—	027	—	029	031	029	026
Mouth:													
Width	070	069	082	076	078	086	086	069	—	082	079	087	072
Height	042	050	051	062	046	051	—	048	—	047	043	046	050
Gills, length:													
1st	045	040	—	—	038	057	—	040	—	049	051	043	057
3d	050	047	—	044	047	055	—	051	—	057	056	048	057
5th	035	046	—	043	050	037	—	045	—	047	045	045	054
Eye (orbit):													
Horizontal	030	029	031	034	047	055	033	031	028	039	034	042	029
Vertical	050	051	048	049	058	—	042	—	044	—	049	050	045
1st dorsal:													
Base	119	117	—	137	101	124	110	112	—	131	122	120	107
Height	129	130	147	144	107	102	128	121	163	147	150	133	152
2d dorsal:													
Base	010	015	—	012	012	018	—	018	—	016	012	015	019
Height	007	—	014	009	009	014	—	007	—	012	010	009	014
Pectoral, anterior margin	343	328	387	380	398	375	356	348	362	393	403	389	324
Pelvic fin:													
Base	164	121	—	169	169	122	—	—	—	—	176	156	155
Height	—	—	—	135	118	—	—	—	—	—	126	128	138
Anal fin:													
Base	017	019	—	016	018	018	018	013	—	025	022	019	022
Height	025	025	—	020	018	020	029	026	—	029	025	031	019
Caudal fin:													
Dorsal lobe	851	792	—	912	905	964	823	864	—	957	1.007	993	839
Ventral lobe	119	118	—	135	132	124	—	127	—	—	137	125	125
Trunk-at-pectoral:													
Height	192	208	—	194	178	178	196	—	—	—	187	181	219
Width	149	135	—	154	160	145	111	—	—	—	151	149	166
Interspace:													
1D-2D	189	171	200	176	189	174	—	—	—	—	191	184	—
2D-caudal	097	072	086	—	—	090	—	128	—	090	094	077	101
Anal-caudal	080	—	052	—	—	037	036	057	—	053	075	054	056

fins, possible misinterpretation of the actual size of these fins in *A. profundus*.

The relative positions of the anal and second dorsal fins vary. The account and illustration of a 130 cm TL *A. superciliosus* from Cuba in Bigelow and Schroeder (1948, figure 5) shows the free rear tip of the second dorsal fin terminating anterior to the anal origin by a distance about equal to the second dorsal base. Nakamura's (1935) illustration of an adult *A. profundus* (pl. 1, figure 1) indicates that the dorsal rear tip extends posterior to the anal base, but his illustration of a fetal *A. profundus* (pl. 2, figure 3) shows that it is about opposite the anal origin. Cadenat (1956, figure 3B-C) illustrated two fetuses of *A. superciliosus* from Senegal, one with the rear tip over the rear end of the anal base and the other with it over the middle of the anal base. Bass et al. (1975, figure 19) pictured a South African specimen of *A. superciliosus* with the tip about over the anal origin. Our 356 cm TL specimen (SHG-A2) from Florida also had the rear tip about opposite the anal origin, but her two fetuses have the rear tip slightly anterior to the anal fin origin. Two specimens from the eastern Central Pacific (SM-9-II-64-3 and LJVC-0355), respectively, had the tip anterior to the anal origin and over the first third of the anal base.

Accounts of bigeye threshers such as those of Springer (1943), Bigelow and Schroeder (1948), Cadenat (1956), Fitch and Craig (1964), Kato et al. (1967), Telles (1970), and Bass et al. (1975), and the specimens examined by us show the pelvic fins to be very large and about the size of the first dorsal fin, but Nakamura's (1935, pl. 1, figure 1) line drawing of an adult female *A. profundus* shows a minute pelvic fin, less than one-fourth of the area of the first dorsal fin. Curiously, the pelvic fins in Nakamura's (pl. 2, figures 3, 4) drawings of a 71 cm fetus of *A. profundus* have the proportions of other bigeye threshers and are about as large in area as the first dorsal fin. Yet Nakamura described the pelvic fins of both adults and fetuses in the same words, "ventral fins moderate" (p. 2, 5). In the absence of pelvic fin measurements in Nakamura's account, we suspect that the unusually small pelvic fins pictured in his adult *A. profundus* may be erroneous and are perhaps due to the difficulties of accurately drawing a large shark, without special techniques and perhaps under trying circumstances (i.e., in a fish market). The drawing of the fetal *A. profundus* seems more accurate and may reflect the writer's ability to study and draw it in his laboratory. Possibly the large adult specimen of *A. pelagicus* sketched by Nakamura (pl. 1, figure 2) was also drawn with undersized pelvics, at least in comparison with the photograph of a specimen by Bass et al. (1975, figure 17), and with photographs and specimens of *A. pelagicus* seen by Compagno. The fetal specimen of "*A. pelagicus*" illustrated by Nakamura (1935, pl. 3) is of no help here as it appears to be a specimen of *A. vulpinus* (unlike the adult).

The supposed differences in the contour of the anterior margin of the first dorsal fin are probably size-related, the contour becoming straighter with increase in size. The adult *A. profundus* pictured by Nakamura (1935) has a nearly straight anterior margin, while in the fetal specimen it is strongly convex. This applies likewise to the 356 cm TL Miami specimen (SHG-A2) of *A. superciliosus* and to the two fetuses taken from her. This change also occurs in *A. vulpinus* (compare the juvenile pictured in Bigelow and Schroeder [1948] with the adult in Bass et al. [1975]) and *A. pelagicus*, as well as some other lamnoid sharks, such as *Isurus oxyrinchus* (Garrick 1967, figure 6).

The lower precaudal pit appears to be variably present or absent in bigeye threshers, as suggested by Bass et al. (1975). The lower pit was present in possibly all of the three adults of *A. profundus*, 332-366 cm TL, studied by Nakamura (1935), though it is not specifically mentioned in his account of a fetal *A. profundus* and not shown in his illustration (pl. 2, figure 1). It was also present in a 372 cm TL adult male from California (CAS-1963-X: 7) studied by Fitch and Craig (1964) but absent in all our Miami specimens and absent in two specimens from the eastern Central Pacific (SM-9-II-64-3 and LJVC-0355). We suspect that the lower precaudal pit is present only in some adult or subadult bigeye threshers, as it has not occurred so far in fetal or very small, free-living specimens. The upper precaudal pit is less well-marked in small specimens than in large subadults and adults.

DESCRIPTIVE NOTES

Proportional measurements of 13 bigeye threshers, including 6 reported by us, are given as proportion of precaudal length in Table 1, rather than total length, as the tail length is apparently quite variable relative to body length. Writers

have previously used precaudal length (Fitch and Craig 1964), total length (Bigelow and Schroeder 1948), and fork length (Stillwell and Casey 1976).

The prominent horizontal head grooves (Figures 3, 4) that are characteristic of *A. superciliosus* are present in all specimens we examined, but are better developed in the large subadults and adults than in the two fetuses taken from SHG-A2. The grooves were not indicated in a 130 cm TL, free-living specimen figured by Bigelow and Schroeder (1948); but we suspect that they were overlooked on this shark although we were not able to examine it. Fitch and Craig (1964) first called attention to these grooves in *A. superciliosus* and noted that similar grooves are also found in teleosts, in the swift, mesopelagic louvars (*Louvarus*) and escolars (*Lepidocybium*). They speculated that the grooves might aid in hydrodynamic flow, thus enabling the bigeye thresher to maneuver more rapidly. Head grooves are absent or poorly developed in other species of threshers.

Another characteristic of the bigeye thresher, at least at sizes above 130 cm TL, are the huge, vertically elongated, fleshy orbits, which are expanded onto the dorsal surface of the head and provide the shark with a dorsal, binocular visual field (Figures 4, 5). The eyes, head grooves, and bulbous, elongated snout of *A. superciliosus* give its head a unique, upward-looking, crested or helmeted appearance. The eyelids (Figure 5) apparently change shape with growth, as our two fetuses, and a 130 cm specimen in Bigelow and Schroeder (1948) have relatively enormous, circular lids without the anteroposterior shortening seen in larger individuals such as the 161 cm immature female pictured by Bass et al. (1975). This change in lid shape is also seen though to a lesser degree in *A. pelagicus*, in which fetuses and small, free-living specimens have circular eyelids and adults more vertically oval lids (Compagno unpubl. obs.).

FIGURE 5.—Lateral view of the left eye of *Alopias superciliosus* (SHG-A7) showing the keyhole shape which may be an adaptation for increasing the dorsal binocular fields. The vertical distance between upper and lower eyelid is 101.5 mm. Photo: S. Spielman.

COLOR

The bigeye thresher is often described as gray (Cadenat 1956; Garrick and Schultz 1963; Bass et al. 1975). Bigelow and Schroeder (1948) stated that the bigeye thresher is "Dark mouse gray above and hardly paler below...," but we suggest that this coloration is true for preserved material and not living or freshly killed specimens. Nakamura (1935) noted that a freshly killed bigeye thresher is purple above, and we observed a violet to purplish cast above fading to creamy white below on the body of the 356 cm TL Miami specimen (SHG-A2). S. Kato and I. Nakamura[6] stated that fresh Central Pacific and eastern Atlantic bigeye threshers are purple-brown or gray-brown dorsally, white, grayish or whitish brown below. In the Miami and Central Pacific specimens a metallic silver or silver blue-green sheen was present on the sides at the level of the gills and on the flanks, as in *A. pelagicus* (Bass et al. 1975) and *A. vulpinus* (Compagno unpubl. data). The ventral surface of the paired fins and the caudal fin is oulined in dark gray.

VERTEBRAE

Vertebral counts have been used as an important character in teleost systematics for many

[6]Susumu Kato (see footnote 3) and Izumi Nakamura (see footnote 4), pers. commun. to L. J. V. Compagno, 1978.

years (i.e., Bailey and Gosline 1955) but their importance in shark systematics was recognized only with the surveys by Springer (1964) and Springer and Garrick (1964). We have compiled available vertebral counts for *A. superciliosus* (Table 2), which includes five of our specimens. The counts indicate that bigeye threshers of the eastern Pacific and Indian Ocean have slightly higher caudal and probably higher total vertebral counts than bigeye threshers from the western North Atlantic. Considerable variation is found in caudal counts in *A. vulpinus* from California (230-254, $n = 8$; Compagno unpubl. data) so that larger samples of vertebral counts of *A. superciliosus* from different regions will be needed to confirm possible population differences.

Vertebrae from the monospondylous precaudal region (centra 30-35) were radiographed in a bigeye thresher (LJVC-0355), in longitudinal view to show the calcification pattern. As with most other lamnoid sharks the dorsal, ventral, and lateral spaces of the intermedialia, between the diagonal uncalcified areas of the basalia, are composed of longitudinal calcified plates or radii that are distally bifurcated and interleaved with cartilage (terminology follows Ridewood 1921). In *A. superciliosus* these radii are fewer and less branched than in either *A. vulpinus* or *A. pelagicus*, and are not basally fused into a solid mass as in *A. pelagicus* (Figure 6).

DENTITION

Another quantitative character often used in shark systematics is the number of tooth rows in each jaw. We give dental formulas for 22 bigeye

TABLE 2.—Vertebral counts of *Alopias superciliosus*.

Number[1]	Size cm (TL)	Maturity	Sex	Locality[1]	Counts[1] MP	DP	PC	DC	TC	Source
—	—	—	—	WNA, New York	—	—	102	190 ± 3	295 ± 3	Springer and Garrick (1964)
GH-A6	340	Adult	Male	WNA, Florida			100	203	303	Original
SHG-A2	356	Adult	Female	WNA, Florida	—	—	102	196	298	Original
SHG-A3	241	Subadult	Male	WNA, Florida	—	—	—	191	—	Original
SHG-A7	356	Adult	Male	WNA, Florida	—	—	102	175	[2]278	Original
UMML-8861	—	Fetus	—	WNA, Florida	—	—	102	180	282	Springer and Garrick (1964)
UMML-8861	—	Fetus	—	WNA, Florida	—	—	102	187	289	Springer and Garrick (1964)
MCZ-36155	63	Fetus	Male	WNA, Cuba	—	—	102	181	283	Springer and Garrick (1964)
USNM-197700	369	Adult	Female	ENP, California	—	—	100	204	304	Springer and Garrick (1964)
LJVC-0355	287	Immature	Female	ECP	66	39	105	196	301	Original
—	161	Immature	Male	SWI, S. Africa	—	—	106	202	308	Bass et al. (1975)
—	363	Adult	Male	SWI, S. Africa	—	—	98	—	—	Bass et al. (1975)

[1]Abbreviations: NUMBER: GH, Hubbell collection; LJVC, L. J. V. Compagno collection; MCZ, Museum of Comparative Zoology, Harvard; SHG, Gruber Collection; UMML, University of Miami Marine Laboratory; USNM, United States National Museum of Natural History, Smithsonian Institution. LOCALITY: ECP, eastern-Central Pacific; ENP, eastern North Pacific; SWI, southwestern Indian Ocean; WNA, western North Atlantic. COUNTS: DC, displospondylous caudal centra; DP, diplospondylous precaudal centra; MP, monospondylous precaudal centra; PC, precaudal (MP + DP) centra; TC, total (MP + DP + DC or PC + DC) centra.
[2]Tail of SHG-A7 noticeably shorter; <49% of the total length.

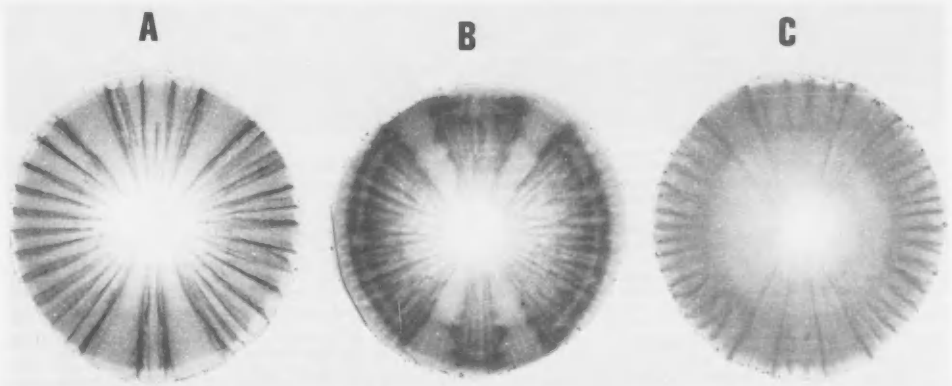

FIGURE 6.—Radiographs in transverse view of the monospondylous vertebral centra of all three *Alopias* species: A, *A. superciliosus*; B, *A. vulpinus*; C, *A. pelagicus*. Note the more simple pattern in *A. superciliosus*. Photo: L. Compagno.

threshers in Table 3, in the form A + B/C + D, where A and B are the numbers of rows in the upper left and right jaw halves, and C and D the numbers in the lower left and right jaw halves. Also presented are total tooth row counts, in the form Ab/Cd, where Ab is the total number of upper rows and Cd the total lower rows. For dental formulas of 10 bigeye threshers the ranges, means, and standard deviations are 11-12 (11.7±0.5) + 10-12 (11.5±0.7)/10-12 (10.8±0.8) + 10-12 (10.7±0.7). For the same number of total counts the ranges, means, and standard deviations are 20-24 (23.2±1.1)/20-24 (21.5±1.4).

Using Applegate's (1965) and Compagno's (1970) terminology for tooth row groups, the dentition of the bigeye thresher can be divided into two rows of anteriors (A) at either side of the symphysis and 8-10 rows of lateroposteriors (LP) on either side and postlateral to them (in both upper and lower jaws, Figure 7). An expanded formula for the bigeye thresher is:

LP9-10 + A2 + A2 + LP8-10/LP8-10
+ A2 + A2 + LP8-10 (Figure 8).

Anterior teeth of threshers differ from lateral and posterior teeth in having narrower crowns relative to their height and more erect cusps, but they are less well differentiated in *Alopias* than in lamnids, odontaspidids, mitsukurinids, and pseudocarchariids. The lateroposterior teeth of the bigeye thresher vary towards the dental band (gradient monognathic heterodonty), becoming smaller, lower relative to width, more oblique-cusped, more convex along the premedial edge, and more deeply notched in the postlateral edge, with the postlateral blade tending to change into cusplets on the more postlateral rows. Posterior teeth are not well differentiated from laterals in the bigeye thresher and are not separated out in the expanded formula; upper intermediate teeth and upper and lower symphyseal teeth are absent.

Teeth in the upper jaw are not markedly different in shape from lowers, but are slightly larger. All teeth are compressed, sharp-edged, and bladelike, and have narrow-based cusps.

Bass et al. (1975) suggested that in *A. superciliosus* the teeth of females are somewhat broader than those of males, reflecting gynandric or sexual heterodonty (dental sexual dimorphism; see Compagno 1970). Comparison of the jaws of an adult female with those of a large adult male (Figures 9, 10) shows that males have teeth (especially the anteriors and more premedial lateroposteriors) with higher, more flexed cusps than females. Gruber and Hubbell[7] (unpubl. data) have examined a number of jaws from male and female

[7]Gordon Hubbell, Director, Candron Park Zoo, Miami, FL 33149.

TABLE 3.—Dental formulas of *Alopias superciliosus*.

Number[1]	Size cm (TL)	Maturity	Sex	Locality[1]	Formula	Total	Source
MCZ-	—	—	—	WNA, Cuba	11 + 11/10 + 10	22/20	Bigelow and Schroeder (1948)
SHG-A2	356	Adult	Female	WNA, Florida	12 + 12/12 + 12	24/24	Original
SHG-A3	290	Subadult	Male	WNA, Florida	12 + 12/11 + 11	24/22	Original
SHG-A4	159	Immature	Male	WNA, North Carolina	12 + 12/11 + 11	24/22	Original
SHG-A5	320	Subadult	Female	WNA, Florida	12 + 11/11 + 11	23/22	Original
SHG-A6	306	Subadult	Female	WNA, Florida	11 + 11/10 + 11	22/21	Original
SHG-A7	356	Mature	Male	WNA, Florida	12 + 12/11 + 10	24/21	Original
GH-A1	—	—	—	WNA, Caribbean	12 + 12/12 + 12	24/24	G. Hubbell (pers. commun.)
GH-A2	381	Mature	Female	WNA, Florida	11 + 11/11 + 11	22/22	G. Hubbell (pers. commun.)
GH-A3	312	Subadult	Female	WNA, Florida	11 + 12/10 + 11	23/21	G. Hubbell (pers. commun.)
GH-A4	342	Mature	Male	WNA, Florida	12 + 12/11 + 11	24/22	G. Hubbell (pers. commun.)
GH-A5	—	—	—	WNA, Florida	12 + 12/11 + 11	24/22	G. Hubbell (pers. commun.)
GH-A6	340	Mature	Male	WNA, Florida	12 + 12/11 + 11	24/22	G. Hubbell (pers. commun.)
MBP-	269	Adult	Male	ENA, Portugal	12 + 12/10 + 10	24/20	Telles[2] (1970)
CBAT-	—	—	—	ESA, Angola	11 + 10/11 + 10	21/21	Telles[2] (1970)
—	400	Adult	Female	ENA, Senegal	10 + 8/ 9 + 8	—	Cadenat[3] (1956)
—	161	Immature	Female	SWI, S. Africa	12 + 11/11 + 11	24/22	Bass et al. (1975)
LACM-F-89	—	—	—	WNP, Japan	12 + 11/11 + 11	23/22	B. Welton (pers. commun.)
CAS-1963-X	372	Adult	Male	ENP, California	11 + 11/10 + 10	22/20	Original[4]
LACM-F-88	378	Adult (?)	Male	ENP, California	12 + 12/10 + 11	24/21	B. Welton (pers. commun.)
LACM-F-90	305	Immature	Female	ENP, California	12 + 12/11 + 11	24/22	B. Welton (pers. commun.)
LJVC-0355	287	Immature	Female	ECP	12 + 12/12 + 11	24/23	Original

[1]Abbreviations: CAS, California Academy of Sciences, San Francisco, Calif.; CBAT, Centro Biologia Aquatica Tropica, Lisbon; GH-A, Gordon Hubbell, *Alopias* jaw collection; LACM, Los Angeles County Museum of Natural History, California; LJVC, L. J. V. Compagno collection; MBP, Museu Bocage, Portugal; MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts; SHG-A, Samuel H. Gruber, *Alopias* collection. WNA, western North Atlantic; ENA, eastern North Atlantic; ESA, eastern South Atlantic; SWI, southwestern Indian; WNP, western North Pacific; ENP, eastern North Pacific; ECP, eastern Central Pacific.
[2]We doubt that this was a mature adult.
[3]Cadenat (1956) mentioned that 1 or 2 teeth were missing on each side of this specimen.
[4]Fitch and Craig (1964) give 9 + 10/10 + 10 for this specimen, but we found that they apparently missed 3 rows of upper teeth.

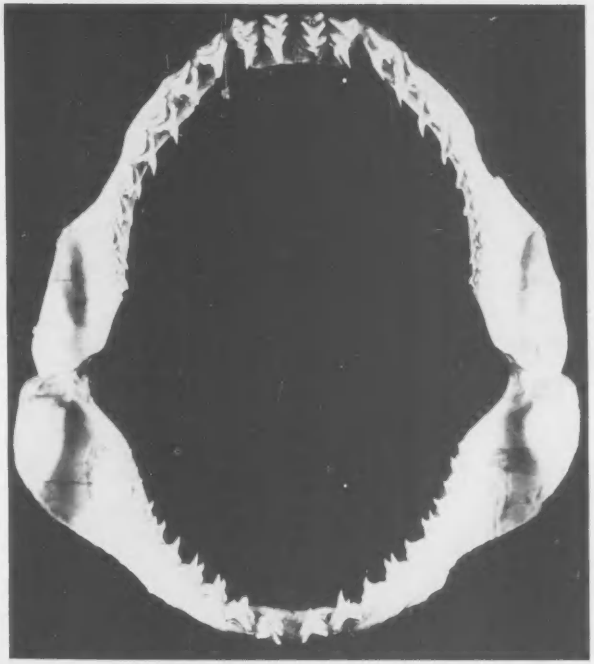

FIGURE 7.—Jaws of 372 cm TL male *Alopias superciliosus* (CAS-Acc. 1963-x: 7). Note the elongated, flexed cusps on the anterior and some lateral teeth which are characteristic of males and shown in detail in Figure 10. Photo: L. Compagno.

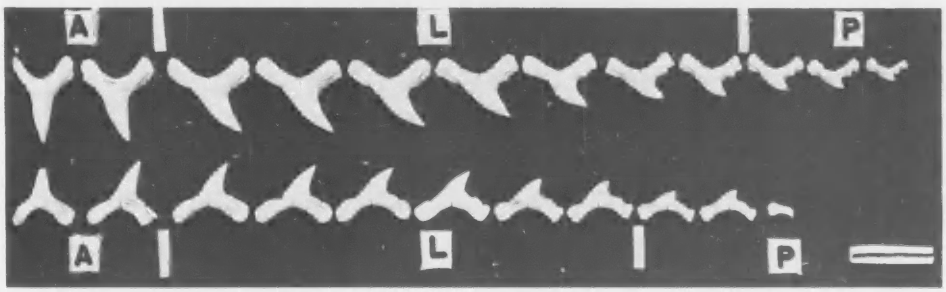

FIGURE 8.—Tooth set from the right side of the jaw of a 278 cm TL female *Alopias superciliosus* (LJVC-0355). A, anterior teeth; L, lateral teeth; P, posterior teeth. Scale mark at lower right is 1 cm. Photo: L. Compagno.

bigeye threshers and have documented this sexual heterodonty. Gynandric heterodonty is found in other sharks (see for example Springer 1964; Springer 1966), and in its ordinary form (teeth larger, more erect, and with larger cusps and often less well developed cusplets in males than in females) may aid the male in holding the female during courtship and copulation (Gruber and Myrberg 1977).

DENTICLES

Samples of skin from the back below the first dorsal fin were removed from three species of threshers (*A. superciliosus*, *A. pelagicus*, and *A. vulpinus*), dried, and examined under the scanning electron microscope to show the structure of their dermal denticles. The lateral trunk denticles of all three species are similar in

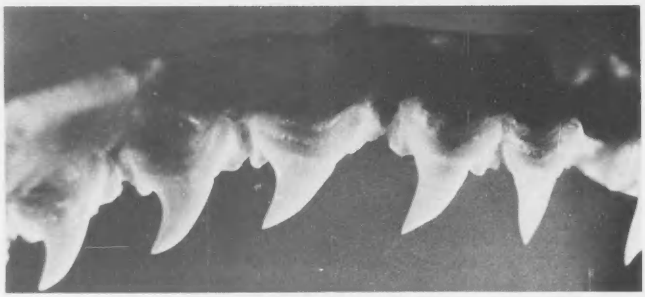

FIGURE 9.—Upper right anterior teeth 1 through 5 of a 381 cm TL female *Alopias superciliosus* (GH-A2) showing that the typical female shape is broader, less sinuous and somewhat flatter than its male counterpart. The cusp height of the 3d anterior tooth was 1.20 cm. Photo: F. Karrenburg.

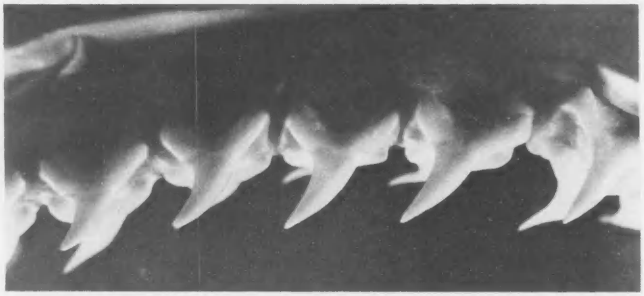

FIGURE 10.—Upper right anterior teeth 1-5 of a 342 cm TL male *Alopias superciliosus* (GH-A4). These elongate, narrrow flexed cusps are typical of males and when compared with the female above one can clearly see the gynandric heterodonty in this species. The cusp height of the third anterior tooth was 1.45 cm. Photo: F. Karrenburg.

having an oval or nearly circular crown with a strong medial ridge and posterior cusp, a pair of weaker lateral ridges, and variably developed lateral cusps (Figure 11). The crowns of these denticles are connected to their bases (buried in the skin) by tall, broad pedicles. The specimen of *A. pelagicus* examined has smaller denticles with less prominent lateral cusps than the two specimens of *A. superciliosus* and three *A. vulpinus* examined.

SIZE

The bigeye thresher grows to a large size as an adult; the heaviest reliably reported was a 284.5 kg female from Cuba (Guitart Manday 1975). Grey (1928) stated that one from New Zealand weighed 640 lb (290 kg). Using the length-weight equation for bigeye threshers given in Guitart Manday (1975)

$$W = 0.1825 \times 10^{-5} L^{3.448534} \text{ or}$$
$$L = 3.448534\,(W/1.825 \times 10^{-6})^{1/2}, \qquad (1)$$

where W is weight in kilograms and L is precaudal length in centimeters; the weight of Guitart Manday's largest bigeye thresher corresponds to a precaudal length of 237 cm and a total length of about 452 cm, while that of Grey's 290 kg bigeye thresher corresponds to a precaudal length of 240 cm and a total length of about 458 cm. Total lengths for these specimens were estimated by averaging the ratio of dorsal caudal and precaudal lengths for 10 specimens of large subadult and adult threshers in Table 1, 270-460 cm TL, which gives $L_{\text{caudal}} = 0.908 \pm 0.079$ SD.$L_{\text{precaudal}}$.

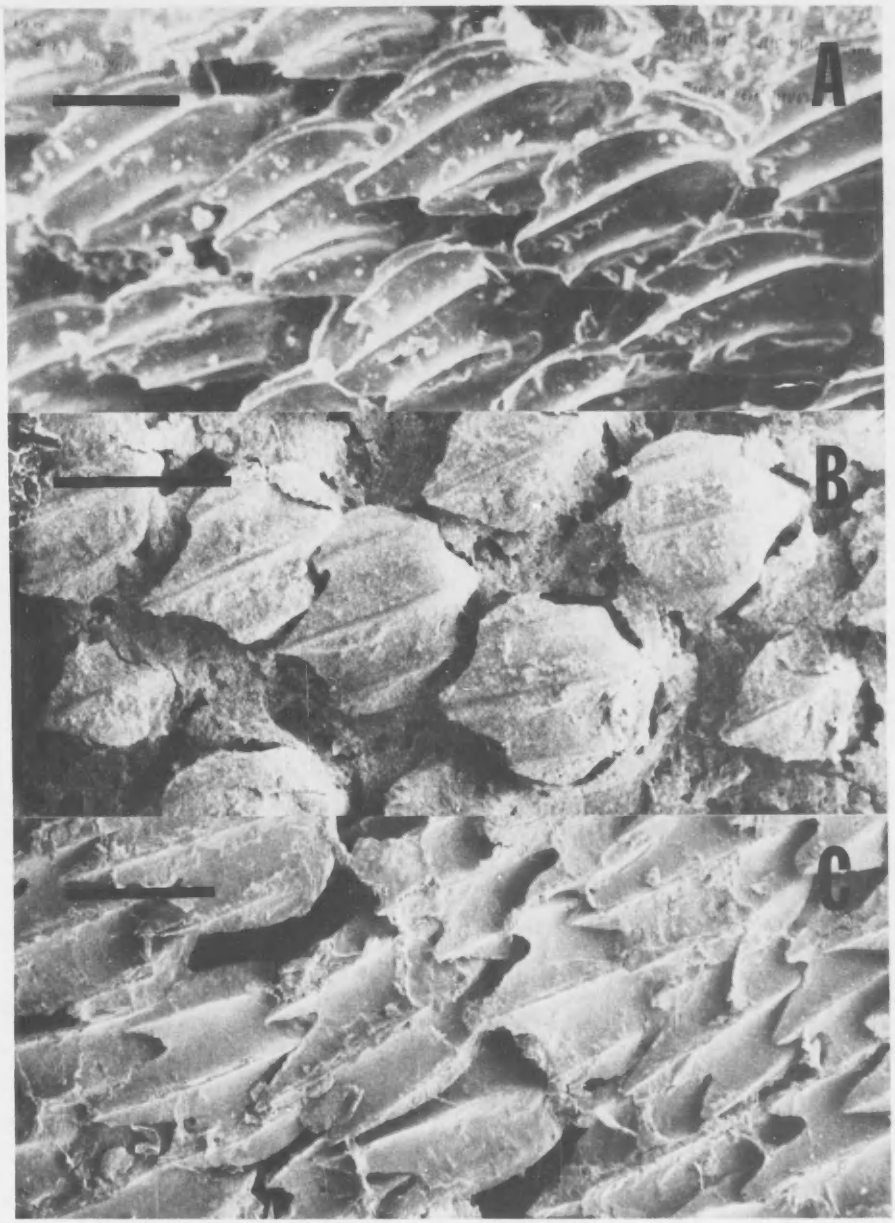

FIGURE 11.—Scanning electron micrographs of thresher lateral trunk denticles. Scale lines (black horizontal bars) equal to 0.1 mm. A, *Alopias superciliosus*, SHG-A2, 356 cm TL adult female. B, *A. pelagicus*, LJVC-0414, 192 cm TL immature male. C, *A. vulpinus*, LJVC-0234, 206 cm TL immature female. Photos: S. Gruber, L. Compagno.

Caudal lengths are variable in the sample mentioned, so that adding and subtracting one standard deviation from the average ratio of caudal to precaudal lengths gives $L_{caudal} = 0.829$ or 0.987 $L_{precaudal}$. Total length given as $L_{total} = L_{precaudal} + 0.908$ (0.829 or 0.987) $L_{precaudal}$. Using the minimum and maximum ratios of caudal to precaudal lengths, Guitart Manday's largest bigeye thresher was estimated to be 434-471 cm long, and Grey's 439-477 cm long.

A bigeye thresher (SHO-16-2) reported by I. Nakamura (pers. commun. to S. Kato[8]) had a precaudal length of 227.2 cm, a dorsal caudal length of 233.5 cm, and a total length (precaudal + dorsal caudal lengths) of 460.7 cm; using Guitart Manday's equation, its precaudal length corresponds to a weight of about 245 kg. Stillwell and Casey (1977) and Cadenat (1956) also measured bigeye threshers of about 4 m TL. However, most adults, especially males, fall below 350 cm TL.

Bigelow and Schroeder (1948) reported a 5.5 m TL bigeye thresher from Cuba, apparently based on data associated with a set of jaws in the collection of Museum of Comparative Zoology, Harvard. It is likely, as Bass et al. (1975) pointed out, that this figure considerably overestimates the maximum size of this shark. The tooth size from Bigelow and Schroeder's (1948) "5.5 m" specimen corresponds almost perfectly to that of a 363 cm TL shark examined by Bass et al. (1975), so that, in the absence of contrary data, the total length of Bigelow and Schroeder's largest specimen should be revised downward to about 360 cm.

The average size of adult females of *A. superciliosus* is larger than males. Guitart Manday (1975) stated that females are always the largest bigeye threshers caught on longlines, many exceeding 250 kg, and averaging 203.8 kg in a sample of eight adults; but males are much smaller, averaging 185.3 kg in a sample of four adults. Stillwell and Casey (1976) reported that 25 females ranged up to 399 cm TL, while the 15 males they examined never exceeded 352 cm TL. However, the mean length of females was only 5 cm greater than that of males. This similarity in average total length resembles a condition noted by Springer (1960) for certain carcharhinid and sphyrnid sharks, in which a small percentage of females in a population grow to a much larger size than most of their sex and species.

[8]Susumu Kato (see footnote 3), pers. commun. to L. J. V. Compagno, 1978.

The longest known adult male bigeye thresher shark was 378 cm TL (LACM-F-88),[9] from off California, and the smallest was 270 cm, from off Portugal (Telles 1970). The longest known adult females are the two of 399 cm TL and about 400 cm TL reported by Stillwell and Casey (1976) and Cadenat (1956) from the western North Atlantic and Senegal, and the shortest two of 355-356 cm from the western North Atlantic (Stillwell and Casey 1976; specimen from Miami, Fla.). The heaviest bigeye thresher reported (Guitart Manday 1975), was a female, presumably mature, and probably over 4.3 m TL (see above).

The smallest free-living bigeye thresher reported to date is a 130 cm TL immature male from off Cuba (Bigelow and Schroeder 1948). Guitart Manday (1975) reported a 144 cm TL free-living individual that weighed 6.7 kg, while Stillwell and Casey (1976) captured a 155 cm TL immature male. We report here a specimen from North Carolina of 159 cm TL. Bigelow and Schroeder (1948) and Osipov (in Gubanov 1979) suggested that parturition occurs in *A. superciliosus* when the fetus attains 64 cm TL, but Cadenat (1956), Nakamura (1935), and Gubanov (1979) reported fetuses respectively at 68, 73, and 100 cm long. Bass et al. (1975) suggested that the most likely size at birth is 100-103 cm TL. Gubanov noted the possibility that larger females might give birth to larger offspring, a possible explanation of the discrepancy of size at birth given by various authors.

Based on available data, the maximum accurately measured total length for *A. superciliosus* is 4.61 m, and weight, 284.5 kg, with total lengths of 4.7-4.8 m and weights of 290+ kg not unlikely. Apparently this species averages smaller in size than at least some populations of *A. vulpinus*, in which females in the western North Atlantic reach 479-549 cm TL; the maximum size for *A. vulpinus* may be over 609 cm TL (Bigelow and Schroeder 1948; Bass et al. 1975).

AGE AND GROWTH

The age of a bigeye thresher has never been determined by standard methods such as analysis of vertebral rings. However, age and growth in other shark species have been investigated by several techniques (i.e., Petersen method, tagging, growth in captivity) and found generally to

[9]Grey's (1928) 4 m bigeye thresher appears to be a male in the published photograph, but the article does not mention the sex.

conform to the von Bertalanffy (1938) model (Wass 1973; Stevens 1975). Holden (1974, 1977) has shown that it is possible, as a first approximation, to obtain parameters for a von Bertalanffy growth curve independently of field data. Using a modification of von Bertalanffy's (1938) basic equation, Holden (1974) rearranged the formula as follows:

$$l_{t+T} - l_t = (L_{\max} - l_t)(1 - e^{-KT}) \qquad (2)$$

where l_t = length at fertilization
l_{t+T} = length at birth
T = gestation period
$L_{\max}$ = maximum observed size
K = growth constant.

We have evaluated these parameters from data given in the literature, and solution of this equation, including generation of the growth curve, was accomplished with computer programs written by Allen (1966).

If Stillwell and Casey (1976) are correct in their assertion in that males mature at 300 cm TL compared with 350 cm TL for females, then time to maturity can be estimated from Figure 12. Assuming parturition in the bigeye thresher at 100 cm (lower curve, Figure 12), then males mature in a little over 3.5 yr while females become sexually active (i.e., reach 350 cm TL) between their fifth and sixth year. Bigeye threshers measuring 4 m TL would be about 10 yr old and the biggest members of this species (480 cm) would be at least 20 yr old.

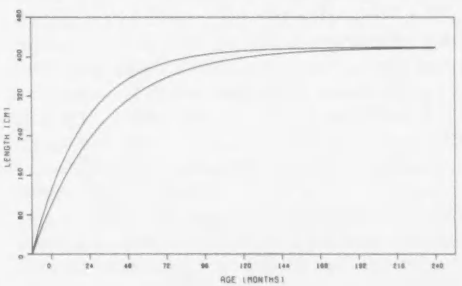

FIGURE 12.—Von Bertalanffy-type growth curve for *Alopias superciliosus*. The curve is based on parameters of: maximum total length of 420 cm; length at birth 100, 130 cm TL and gestation period of 12 months. The lower and upper curves represent a growth rate in sharks born at 100 and 130 cm TL, respectively. If this model is correct, males mature in approximately 3½ yr compared to 4½ yr for females. The largest of these sharks would be between 10 and 20 yr of age.

It should be reemphasized that this curve is but a first approximation since the assumptions of the von Bertalanffy model may not actually be satisfied by growth of the bigeye thresher. Thus this curve cannot substitute for field data and must be validated by independent methods.

No previous attempts have been made to determine the age of a bigeye thresher. We stained a few vertebral centra of the bigeye thresher LJVC-0355—287 cm TL female—from the monospondylous precaudal region (centra 30-31, 33, as counted from the head) using the alizarin technique of LaMarca (1966) and the silver nitrate technique of Stevens (1975), to demonstrate growth rings on the inner surfaces of the calcified double cones. This technique revealed a central clear area surrounded by at least eight dark rings concentric with and interspaced by lighter rings (Figure 13). The clear area is about 14.1 mm across, and the double cone 25.2 mm in horizontal diameter in centrum 33. It is not known if the dark rings are annual (added once a year), but presumably the central clear area represents the maximum size of the fetal vertebral centrum.

A comparison of Figure 12 with the data given in Figure 13 shows that if the rings are annual, the von Bertalanffy model considerably underestimates rate of growth in the bigeye thresher. However, we are not aware of any published work showing that growth rings in the centrum of warm-water sharks are annual. Several temperate water elasmobranchs lay down annual growth rings but the (temperate water) basking shark, *Cetorhinus maximus*, forms a pair of rings each year (Tanaka and Mizue 1979). So in the absence of some confirming data giving the interval between ring formation, we cannot estimate the age of the bigeye thresher by counting circuli in the vertebral centrum.

Beside the length-weight relations developed by Guitart Manday (1975) and Stillwell and Casey (1976), the only other growth data are deductions made by Stillwell and Casey concerning allometry. Based on measurements from 12 adult bigeye threshers (8 males, 4 females) they concluded that head, eye, and mouth dimensions become proportionally shorter as growth proceeds. In contrast, the height of the first dorsal, interspaces between fins, and clasper length all increase. Some differences between males and females in proportional growth were noted in their study.

Data from several sources (Nakamura 1935; Springer 1943; Bigelow and Schroeder 1948;

FIGURE 13.—Centrum 33 from a 287 cm TL, 59 kg female *Alopias superciliosus* (LJVC-0355) treated with the silver nitrate technique of Stevens (1975). This method intensifies the calcified growth rings as shown, for easy visualization. At least 8 and probably 11 dark rings surround a central clear area of 14.1 mm. The external diameter of centrum 33 is 25.2 mm. Photo: L. Compagno.

Cadenat 1956; Bass et al. 1975), but primarily Stillwell and Casey (1976), indicate that males mature at about 300 cm TL, while females mature at a larger size, probably 350 cm TL. To these data are added the observation that all males over 307 cm TL examined by Stillwell and Casey had calcified, elongate claspers, and mature sperm in the epididymis. They noted that a smaller male of 289 cm TL had nearly mature testes.

In contrast, of 13 females examined by Stillwell and Casey (1976), only those over 350 cm TL possessed mature ova and enlarged ovaries. These data support earlier studies indicating that mature (pregnant) females are all larger than about 350 cm TL. Guitart Manday (1975) noted that only the largest females captured in the Cuban fishery were pregnant. Finally, the size of our pregnant female (356 cm TL) agrees with the concept of female maturity at about 350 cm TL.

ABUNDANCE, DISTRIBUTION, AND HABITAT

The early literature on the bigeye thresher seemed to indicate that it is a widely distributed but rare, subtropical to tropical pelagic shark inhabiting relatively deep water. For example, Telles (1970) believed that only 20 bigeye threshers had ever been recorded. Nakamura (1935), Bigelow and Schroeder (1948), Cadenat (1956), and others suggested that *A. superciliosus* was a deepwater species, and Springer (1963) reported that it never approached to within a few hundred meters of the surface. More recent data based on longline catches point to localized concentrations of this species in considerable numbers, especially in the western North-Central Atlantic from off the north coast of Cuba and off North Carolina (Guitart Manday 1975; Stillwell and Casey 1976), and in the northwestern Indian Ocean (Osipov 1968; Gubanov 1972). Enough occur off Cuba to have yielded a total commercial catch for 1975 of 3,400 kg (Guitart Manday[10]). In the western Central Atlantic the species occurs north at least to off New York (Schwartz and Burgess 1975; Stillwell and Casey 1976) and apparently is relatively eurythermic. In the western North Atlantic bigeye threshers are usually caught in waters with the surface temperature from 16° to 25° C, and with longlines fished at a depth from slightly below the surface to 65 m depth where the temperature falls to 14° C (Stillwell and Casey 1976).

The bigeye thresher may be able to maintain body temperatures higher than ambient water temperature (Carey et al. 1971), which may equip it for incursions into colder water. However, like the shortfin mako, *Isurus oxyrinchus*, which is also partly homeothermic, the bigeye thresher is apparently a species preferring warm temperate to tropical waters. From available distributional data the bigeye thresher does not occur in cold temperate waters and apparently has a narrower temperature and latitudinal range than either the blue shark, *Prionace glauca*, or the great white shark, *Carcharodon carcharias*, both of which range from cold temperate seas into the tropics.

[10]Dario Guitart Manday, Institute of Oceanology, Academy of Science of Cuba, Havana, Cuba, pers. commun. to S. H. Gruber, 24 January 1978.

Alopias superciliosus is both neritic and pelagic. Kato et al. (1967) and S. Kato (footnote 8) noted that the bigeye thresher is commonly caught on high-seas longlines far from land, but capture data in Cadenat (1956), Strasburg (1958), Fitch and Craig (1964), Osipov (1968), Guitart Manday (1975), and Stillwell and Casey (1976) indicate that concentrations of the species commonly occur near land and that it occasionally enters coastal and even shallow waters. It also occurs near the bottom in relatively deep water (Nakamura 1935; Fitch and Craig 1964), has been captured at the surface offshore (the Miami specimen), and is known to range to a depth of about 500 m. Prey items taken from stomachs of the bigeye thresher include both midwater and benthic species indicating the habitats visited by the shark (see below for details).

Figure 14 is a map of the known distribution of *A. superciliosus*, including approximate numbers collected. The range as presently known includes the western North Atlantic from off New York to Florida, the Bahamas, Cuba, and the Caribbean to at least Venezuela (Springer 1943; Bigelow and Schroeder 1948; Fitch and Craig 1964; Mago L. 1970; Schwartz and Burgess 1975; Stillwell and Casey 1976; Compagno 1978). It occurs in the western South Atlantic from off southern Brazil (Sadowsky and Amorim 1977); the eastern Atlantic from off Portugal, Madeira, Senegal, possibly Guinea or Sierra Leone, Angola, and the Mediterranean (Lowe 1840; Cadenat 1956, 1961; Williams 1968; Telles 1970; and authors' specimens); the western Indian Ocean from off South Africa, Madagascar, and the Arabian Sea (Fourmanoir 1963; Osipov 1968; Gubanov 1972; Bass et al. 1975); the western Pacific from off Taiwan, possibly Japan, New Caledonia, and New Zealand (Grey 1928; Nakamura 1935; Fourmanoir and Rancurel 1972; and authors' specimens); the central Pacific, north and south of the Hawaiian Islands and between Panama and the Marquesas Islands (Strasburg 1958; S. Kato footnote 8); and the eastern Pacific from off southern California (Fitch and Craig 1964) and in the Gulf of California (Applegate et al. 1979).

REPRODUCTION

Intrauterine development in thresher sharks is ovoviviparous. As in the lamnids and odontaspidids, fetal bigeye threshers are apparently

FIGURE 14.—Distribution of *Alopias superciliosus*. The 16 filled circles represent stations where fewer than 10 bigeye threshers were collected. The four filled squares show stations where this shark has been taken in commercial numbers. Several more Bahamian locales reported by the U.S. National Marine Fisheries Service were not included because the scale on the map is too coarse. This chart does not include much of the Soviet or Japanese longline catch, but extends the known distributon of *A. superciliosus* to the Mediterranean and New Zealand.

ovophagous. Horny infertile eggs are deposited in each oviduct and the embryo consumes these as development proceeds (Cadenat 1956; Gubanov 1972). Figures 15 and 16 show the embryos and the infertile eggs removed from the oviducts of specimen SHG-A2. Curiously, Gubanov (1979) claimed that the eggs of the bigeye thresher differ considerably from those of the common thresher. However, the eggs shown in our Figure 11b appear almost exactly like those shown in Gubanov's figure 1. Yet the eggs shown in Gubanov's figure 1 were said to be characteristic of the common thresher only. A possible explanation of this discrepancy is that Gubanov's figures 1 and 2 actually represent nutritive and fertile eggs, which might be similar in both species.

Most sharks do not acquire functional teeth until they reach a size close to that at parturition. However, both of our immature fetuses (Figure 15) had fully functional teeth, which is quite unusual among sharks. Perhaps the early formation of teeth aids the fetal bigeye thresher in cannabalizing potential siblings. Yet, fetal pelagic thresher *A. pelagicus* does not acquire functional teeth until it reaches considerably larger size than our two bigeye thresher fetuses.

As is often the case in odontaspidids and lamnids, the bigeye and other threshers produce only two well-developed offspring per pregnancy. While Guitart Manday (1975) mentioned one or two embryos in each oviduct the usual number is a single fetus in each oviduct (Nakamura 1935;

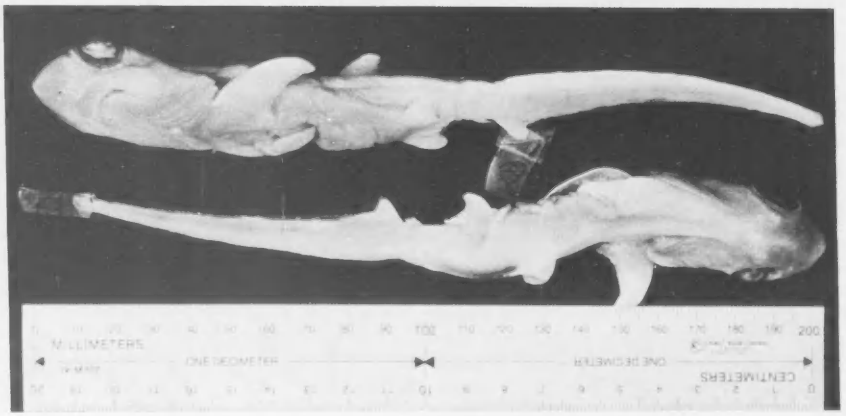

FIGURE 15.—Embryos removed from the specimen shown in Figures 1 and 2. As shown, they are approximately 206 mm TL and are probably in the first trimester of development. Photo: S. Gruber.

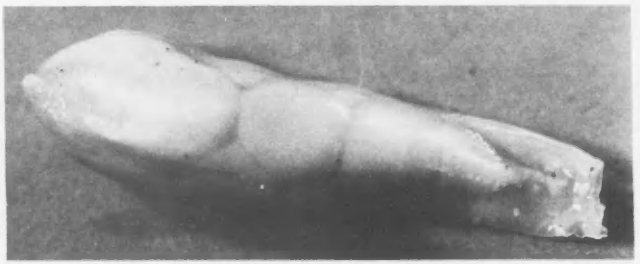

FIGURE 16.—Infertile, horny eggs of *Alopias superciliosus* (SHG-A2) found in the oviducts along with the embryos. Thresher embryos are thought to consume the nutritive, yolk-filled eggs during development (ovophagy). Photo: F. Karrenburg.

Springer 1943; Cadenat 1956; etc.). Since the gestation period is probably 12 mo (Holden 1974), the reproductive capacity of this shark may be said to be relatively low.

Guitart Manday (1975) reported that most large females throughout the year contained embryos. If the reproductive pattern is similar to that of the common thresher (Gubanov 1972, 1979), then mating occurs throughout the year. Not enough data are available for the bigeye thresher to demonstrate seasonality. However, most of the large females examined have been pregnant.

FOOD

Stomach contents of bigeye threshers have been reported in only three studies: Fitch and Craig (1964) obtained some 5 kg of Pacific whiting, *Merluccius productus*, a benthic teleost, from the stomach of their specimen; Bass et al. (1975) reported that a bigeye thresher captured in the protective shark nets along the beach at Durban (hardly deep water) had recently eaten another elasmobranch, perhaps also fouled in the net; Stillwell and Casey (1976) examined the stomachs of 35 bigeye threshers and found over 50% to have food remains—squid was the most common food, composing some 66% of the stomach contents. Other prey included remains of pelagic teleosts, such as scombrids, alepisaurids, clupeids, and istiophorids.

Stomach contents recovered from one of our specimens (SHG-A2) consisted of several eye lenses and two pairs of squid beaks. These were identified by Gilbert Voss[11] as ommastrephid remains, probably from the genus *Illex*. Voss mentioned that *Illex* made up 75-80% of the cephalopod diet of the swordfish, *Xiphias gladius*, caught in the Florida Current.

The food of the bigeye thresher thus consists of small to moderate benthic and pelagic teleost fish, crustaceans, and cephalopds, and as presently known, is restricted to a few species.

PREY CATCHING

According to Springer (1961) the upper caudal lobe of *Alopias* (along with the armed rostrum of the pristiophorids *Pristiophorus* and *Pliotrema*) are the only structures of modern sharks functioning specifically for killing prey (jaws and teeth being used for other purposes in addition to feeding). However, it has not been universally accepted that the tail of thresher sharks is actually used in feeding. In an interesting discussion of this controversy, Lineweaver and Backus (1969) noted that the ichthyologists J. T. Nichols and C. M. Breder doubted that the tail was sufficiently rigid or muscular to kill prey.

Grossly overdeveloped appendages such as the claw of the male fiddler crab, *Uca* sp., often evolve along with elaborate courtship signals, and it is possible that the elongated tail of *Alopias* evolved in the context of a social or species recognition signal. However, field observations support Springer's (1961) concept of the thresher's tail as an offensive weapon for prey capture. One of the first such observations is that of Blake-Knox (1866), who claimed that a common thresher, *A. vulpinus*, used its caudal fin to kill a loon and then consumed the bird. Coles (1915) reported common threshers as feeding in shallow water by throwing fish into their mouth with their caudal fins. Allen (1923) gave a similar detailed description of the feeding behavior of a common thresher. Grey (1928) observed common threshers following baits trolled from a sport fishing boat and striking at the bait with their tails.

Recently, indirect but compelling observations from longline fisheries confirm that threshers use their tail in feeding. Gubanov (1972) reported that 97% of all three thresher species captured were foul-hooked in the upper caudal. This agrees with Stillwell and Casey (1976), who noted that several bigeye threshers were tail-hooked and that two or more baits were often recovered from a captured bigeye thresher's stomach. This suggested to Stillwell and Casey as well as to Gubanov that the live baits were dislodged from the hooks probably by blows from the thresher's caudal fin.

EXPERIMENTAL STUDIES

The bigeye thresher has occasionally been the subject of study unrelated to fishery, natural history, or taxonomic observation. Carey et al. (1971) measured the muscle temperature of a number of freshly captured sharks and teleosts and concluded that, among others, the bigeye thresher is warm-bodied. They described a single vascular heat exchanger which probably makes the storage of heat possible in this species.

[11]Gilbert Voss, Professor of Biology and Living Resources, RSMAS, University of Miami, Miami, FL 33149, pers. commun. to S. H. Gruber, December 1979.

Okada et al. (1969) removed the brain from *A. superciliosus* and compared it with the brains of a number of other sharks in an effort to discern a common structural pattern which might be related to ecology or predatory behavior. They concluded that brain morphology correlates with ecology and behavior rather than with taxonomic similarity since distantly related shark species sharing similar behavior and habitat shared in the development of a number of homologous brain structures. According to Okada et al. the optic tectum of *A. superciliosus* is well developed compared with that of the common thresher and mako, *Isurus*. Perhaps most noteworthy was the size of the cerebellum, which was even larger than the telencephalon. The reverse is usually found (Figure 17). The brain of a 3 m *A. superciliosus* weighed approximately 30 g, some one-third heavier than that of a 3.6 m *A. vulpinus*. The heavier brain of *A. superciliosus* reflects the prominence of the optic lobes. Speculations as to the significance of these structures would be premature because of the paucity of physiological data on shark brains.

Two further studies have used the bigeye thresher as a laboratory subject. Bundschuh and Ballester (1971) tested the serum of 10 shark species including the bigeye thresher for antibodies against human saliva, erythrocytes, and serum. Natural antibodies against human proteins were reported, although the significance of these antibodies was unclear. Finally, Gabeva and Kovaleva (1976) described morphological changes associated with spermatogenesis in the bigeye thresher, and the role of the follicular epithelium of the testes in the process.

The dearth of experimental studies on the bigeye thresher points to the difficulty of obtaining fresh material for detailed analysis. Because of this and because the bigeye thresher has never been kept in captivity, it does not ordinarily make a suitable subject for experimental or detailed study.

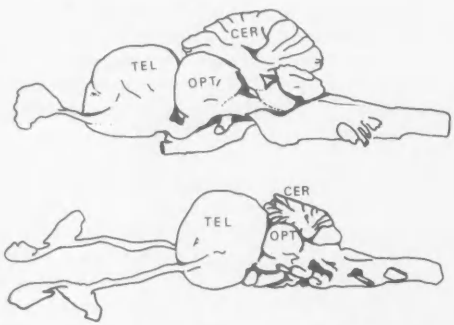

FIGURE 17.—Lateral views of the brains of *Alopias superciliosus* (upper) and *Carcharhinus* sp. (lower) after Okada et al. (1969). Brains have been sketched with telencephalon (TEL) the same size. Note that the optic tectum (OPT) and cerebellum (CER) are relatively much larger in the bigeye thresher.

PARASITOLOGY

The known parasite fauna of the bigeye thresher has been given in five papers: three on gut cestodes and two on external copepods. Dailey (1969) erected the order Litobothridea to include some unusual tapeworms he found in massive infections of the spiral valve of two bigeye threshers collected in southern California. Two worms, *Litobothrium alopias* and *L. coniformis*, were described as new species. Kurochkin and Slankis (1973) further described *L. daileyi* and *Renyxa amplifica* from the spiral valve of bigeye threshers also from the Pacific Ocean. Thus, it would appear that this group of cestodes has evolved along with the Alopiidae and may be restricted to that family. Finally, Heinz and Dailey (1974) reported two cestodes from the stomach of the bigeye thresher: *Sphyriocephalus viridis* and *S. pelorosoma*, the latter a new species.

The only other parasites reported from the bigeye thresher were two new species of copepods: *Pagina tunica* and *Bariaka alopiae*. *Pagina tunicata* was removed from the body surface while *B. alopiae* was taken from the gills (Cressey 1964, 1966). Cressey collected the type-specimen of *B. alopiae* from bigeye threshers captured off Madagascar and South America at stations separated by almost 20,000 km. Because of this great distance Cressey speculated that *B. alopiae* has a specific affinity for the bigeye thresher.

These few species probably do not represent a complete catalogue of parasites infecting the bigeye thresher, but rather are noteworthy examples. If the bigeye thresher is similar to other shark species, it harbors a diverse assemblage of macroparasites including cestodes, nematodes, leeches, copepods, and amphipods.

COMMERCIAL IMPORTANCE

Commercial exploitation of threshers, especially the bigeye thresher, follows two fishery

patterns. The first, exemplified by methods of the Japanese and Soviet high-seas pelagic fleet, involves highly mobile longline fishing vessels which actively seek out concentrations of predatory fish associated with small-scale oceanographic processes, such as plankton concentrations, and local circulation patterns (Osipov 1968; Gubanov 1972). While tunas are the major objective of these fisheries, sharks and billfishes are an important bycatch.

Osipov (1968) noted that, in the northwestern Indian Ocean, local circulation patterns produce distinct areas of plankton and fish concentrations in which one or two predatory species predominate. These associations are dynamic both in species composition and time. Thus the concentration of any species in such an area is both spatially and temporally discontinuous and falls off rapidly outside the enrichment cells. As a consequence, fishing vessels must move continuously in the wake of fish schools as concentrations form and disperse.

Osipov (1968) identified three such areas in the Indian Ocean off the Republic of Somalia. In one of these plankton-enriched areas carcharhinid sharks predominated, while the bigeye thresher was the most plentiful shark in another. Taken overall, however, the bigeye thresher amounted to only 12% of the total shark catch. Thus, while the distribution of *A. superciliosus* on the high seas is patchy, they make up a reasonable proportion (over 10%) of the shark catch, at least seasonally.

The bigeye thresher is also commercially important in the short-range pelagic fishery operating off the northwestern coast of Cuba (Guitart Manday 1975, footnote 10). However, the pattern of distribution is quite different from that in the Indian Ocean. Longlines are set year round in the Cuban fishery and 11 shark species are caught in commercially exploitable numbers. Of 11 species, the bigeye thresher is the third most abundant and amounted to some 20% by weight of the total 1973 shark catch. The Cubans have been fishing this species more effectively in recent years and have doubled their catch between 1971 and 1975.

Seasonal distribution is also evident in the Cuban catch records (Guitart Manday 1975). The poorest catches are in March-June. The catch of bigeye threshers gradually increases over the summer and peaks in the fall around September-October, to decline again in the winter.

Bigeye threshers occasionally enter the market when they are caught by sport and commercial anglers fishing for swordfish off southeastern Florida. Since both species are caught at night near the surface in the Florida Current it is not surprising to see several bigeye threshers each year captured by commercial longliners or during the swordfish tourneys. Incidentally, many of these animals are foul-hooked as described above, perhaps reflecting a preference to attack bait with their caudal fins. However, in this fishery the hook is usually attached to a nylon monofilament leader specifically to avoid catching sharks. Thus the low incidence of mouth hooked bigeye threshers could reflect losses due to biting through the leader.

Finally, this species has been captured a few times in gill nets set at moderate depth, to 160 m (Fitch and Craig 1964; Telles 1970; Bass et al. 1975).

ACKNOWLEDGMENTS

This investigation was supported by grants from the Biological Oceanography Section of NSF (OCE-78-26819) and ONR-Oceanic Biology (N00014-75-C-0173) to S. H. Gruber and by a writer's grant from FAO to L. J. V. Compagno. We wish to thank Gloria Lerma for her assistance in the literature surveys; Bruce Welton, Pearl Sonada, Stewart Springer, and Gordon Hubbell for providing specimens and dried jaws from their extensive collections; Joan Brownell and Eugene Flipse for the X-ray analyses; Fred Karrenburg for preparing the photographs in Figures 1, 2, and 3; Marie Gruber for rendering the line drawings; and Denise Hurley and Helena Detorres for typing the final copy.

We are also grateful to Pflueger Taxidermy, Inc., especially Susie Hass, Ralph Grady, and Tim Master, for informing us whenever a bigeye thresher was received for taxidermy. We thank Bill Harrison and Dan Kipnis for collecting several fresh bigeye threshers for us.

We thank John Fitch for pointing out the Zane Grey article and Izumi Nakamura for the Mediterranean record. We especially thank Susumu Kato for providing us with his complete bigeye thresher records and Dario Guitart Manday for providing unpublished data from the Cuban longline fishery.

Finally, we are grateful to C. Richard Robins and Donald P. de Sylva for critically reading this manuscript and providing many thoughtful improvements.

LITERATURE CITED

ALLEN, K. R.
1966. A method of fitting growth curves of the von Bertalanffy type to observed data. J. Fish. Res. Board Can. 23:163-179.

ALLEN, W. E.
1923. Behavior of the thresher shark. Science 63:31-32.

APPLEGATE, S. P.
1965. Tooth terminology and variation in sharks with special reference to the sand shark, *Carcharias taurus* Rafinesque. Los Ang. Cty. Mus., Contrib. Sci. 86, 18 p.

APPLEGATE, S. P., L. ESPINOSA A., L. B. MENCSACA L., AND F. SOTELO M.
1979. Tiburones Mexicanos. Subsecretaria de Educacion e Investigagion Teconologicas, Mexico City, 146 p.

BAILEY, R. M., AND W. H. GOSLINE.
1955. Variation and systematic significance of vertebral counts in the American fishes of the family Percidae. Univ. Mich. Mus. Zool. Misc. Publ. 93, 44 p.

BASS, A. J., J. D. D'AUBREY, AND N. KISTNASAMY.
1975. Sharks of the east coast of southern Africa. IV. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhinicodontidae. Oceanogr. Res. Inst. (Durban) Invest. Rep. 39, 102 p.

BERTALANFFY, L. VON.
1938. A quantitative theory of organic growth (Inquiries on growth laws II). Hum. Biol. 10:181-213.

BIGELOW, H. B., AND W. C. SCHROEDER.
1948. Sharks. *In* A. E. Parr and Y. H. Olsen (editors), Fishes of the western North Atlantic. Part one, p. 59-546. Mem. Sears. Found. Mar. Res., Yale Univ.

BLAKE-KNOX, H.
1866. Glances into the ichthyology of the county of Dublin. Zool. 1:505-510. [Cited from Lineweaver and Backus (1969).]

BONNATERRE, J. P.
1788. Tableau Encyclopedique et Méthodique des Trois Règnes de la Nature... Ichthyologie. Chez Panckoucke, Paris, 215 p.

BUNDSCHUH, G. VON, AND J. M. BALLESTER.
1971. Agglutination menschlicher Erythrozyten durch Serum verschiedener Haifischarten. Biol. Zbl. 90:321-329.

CADENAT, J.
1956. Note d'Ichtyologie ouest-africaine. XV.—Sur un Requin-Renard nouveau pour la faune d'Afrique Occidentale française *Alopias superciliosus* (Lowe) 1840? Bull. Inst. Fr. Afr. Noire 18 A:1257-1266.
1961. Notes d'Ichthyologie ouest-africaine XXXIV. Liste complémentaire des espèces de poissons de mer (provenant des côtes de l'Afrique occidentale) en collection à la section de biologie marine de l'I.F.A.N. à Gorée. Bull. Inst. Fr. Afr. Noire 23A:231-245.

CAREY, F. G., J. M. TEAL, J. W. KANWISHER, K. D. LAWSON, AND J. S. BECKETT.
1971. Warm-bodied fish. Am. Zool. 11:135-143.

CHEN, J. T. F.
1963. A review of the sharks of Taiwan. Biol. Bull. Dep. Biol. Coll. Sci., Tunghai Univ., Ichthyol. Ser. 1, 19:1-102.

COLES, R. J.
1915. Notes on the sharks and rays of Cape Lookout, N.C.. Proc. Biol. Soc. Wash. 28:89-94.

COMPAGNO, L. J. V.
1970. Systematics of the genus *Hemitriakis* (Selachii: Carcharhinidae), and related genera. Proc. Calif. Acad. Sci., Ser. 4, 38:63-98.
1978. Family: Alopiidae. *Alopias superciliosus*. *In* W. Fischer (editor), FAO species identification sheets for fishery purposes, Western Central Atlantic (fishing area 31). Vol. 5, unpaged. FAO, Rome.

CRESSEY, R. F.
1964. A new genus of copepods (*Caligoida*, *Pandaridae*) from a thresher shark in Madagascar. Cah. ORSTOM-Oceanogr. Ser. Nosy Be 2(6):385-397.
1966. *Bariaka alopiae* n. gen., n. sp. (*Copepoda*: *Caligoida*), a parasite on the gills of a thresher shark. Bull. Mar. Sci. 16:324-329.

DAILEY, M. D.
1969. *Litobothrium alopias* and *L. coniformis*, two new cestodes representing a new order from elasmobranch fishes. Proc. Helminth. Soc. Wash. 36:218-224.

DUMÉRIL, A.
1865. Histoire naturelle des poissons ou ichthyologie general. Vol. I and II. Libraire Encyclopedique, Paris, 120 p.

FITCH, J. E., AND W. L. CRAIG.
1964. First records for the bigeye thresher (*Alopias superciliosus*) and slender tuna (*Allothunnus fallai*) from California, with notes on eastern Pacific scombrid otoliths. Calif. Fish Game 50:195-206.

FOURMANOIR, P.
1963. Raies et requins-scie de la cote ouest de Madagascar (ordre des Batoidei). [Bibliogr. Engl.] Cah. ORSTOM-Oceanogr. Ser. Nosy Be 1(6):33-58.

FOURMANOIR, P., AND P. RANCUREL.
1972. Sharks of New Caledonia. [Abstr.] Int. Symp. Oceanogr. South Pac., Wellington, N.Z., 1972, p. 516.

FOWLER, H. W.
1936. The marine fishes of West Africa, based on the collection of the American Museum Congo Expedition, 1909-1915. Bull. Am. Mus. Nat. Hist. 70(1):1-605.
1941. Contributions to the biology of the Philippine archipelago and adjacent regions. U.S. Nat. Mus. Bull. 13(100), 879 p.

GABEVA, N. S., AND T. J. KOVALEVA.
1976. On the morphodynamics of the follicular cells (Sertoli cells) in spermatogenesis of lamellibranchiate fish (subclass Elasmobranchii). (O morfodinamike follikulyatnykh kletok (Kletok Sertoli) spermatogeneze plastinozhabernykh ryb (podklass Elasmobranchii).) Vestn. Univ. Leningr. Ser. Biol. 1(3):50-58.

GARMAN, S.
1913. The Plagiostomia (sharks, skates and rays). Mem. Mus. Comp. Zool. Harvard Coll. 36, 151 p.

GARRICK, J. A. F.
1967. Revision of sharks of genus *Isurus* with description of a new species (Galeoidea, Lamnidae). Proc. U.S. Natl. Mus. 118:663-690.

GARRICK, J. A., AND L. P. SCHULTZ.
1963. A guide to the kinds of potentially dangerous sharks. *In* P. W. Gilbert (editor), sharks and survival, p. 3-60. D. C. Heath Co., Boston.

GREY, Z.
1928. Big game fishing in New Zealand seas. Nat. Hist. 28(1):46-52.

GRUBER, S. H., AND A. A. MYRBERG, JR.
1977. Approaches to the study of the behavior of sharks. Am. Zool. 17:471-486.

GUBANOV, YE. P.
1972. On the biology of the thresher shark [*Alopias vulpinus* (Bonnaterre)] in the Northwest Indian Ocean. J. Ichthyol. 12:591-600.
1979. The reproduction of some species of pelagic sharks from the equatorial zone of the Indian Ocean. J. Ichthyol. 18:781-792.

GUITART MANDAY, D.
1975. Las pesquerias pelagico-oceanicas de corto radio de accion en la region noroccidental de Cuba. Acad. Cienc. Cuba Ser. Oceanol. 31, 26 p.

GÜNTHER, A.
1870. Catalogue of the fishes in the British Museum. Vol. 8. Catalogue of the Physostomi, containing the families Gymnotidae, Symbranchidae, Muraenidae, Pegasidae, and of the Lophobranchii, Plectognathi, Dipnoi, Ganoidei, Chondropterygii, Cyclostomata, Leptocardii in the British Museum. Br. Mus., Lond., 549 p.

HEINZ, M. L., AND M. D. DAILEY.
1974. The Trypanorhyncha (Cestoda) of elasmobranch fishes from southern California and northern Mexico. Proc. Helminth. Soc. Wash. 41:161-169.

HOLDEN, M. J.
1974. Problems in the rational exploitation of elasmobranch populations and some suggested solutions. *In* F. Hardin-Jones (editor), Sea fisheries research, p. 187-215. Logos Press, Lond.
1977. Elasmobranchs. *In* J. A. Gulland (editor), Fish population dynamics, p. 187-215. Wiley, Lond.

KATO, S., S. SPRINGER, AND M. H. WAGNER.
1967. Field guide to eastern Pacific and Hawaiian sharks. U.S. Fish Wildl. Serv., Circ. 271, 47 p.

KUROCHKIN, YU. B., AND A. J. SLANKIS.
1973. Novye predstavitele i sostav otryada Litobothridea Dailey, 1969 (Cestoidea). (New representative and composition of the order Litobothridea Dailey, 1969 (Cestoidea).) [In Russ.] Parazitologiya (Leningr.) 7(6):502-508.

LAMARCA, M. J.
1966. A simple technique for demonstrating calcified annuli in the vertebrae of large elasmobranchs. Copeia 1966: 351-352.

LINEWEAVER, T. H., AND R. H. BACKUS.
1969. The natural history of sharks. J. B. Lippincott Co., Phila., 256 p.

LOWE, R. T.
1840. On new species of fishes from Madeira. Proc. Zool. Soc. Lond. 8:36-39.

MAGO L., F.
1970. Lista de los Peces de Venezuela incluyendo un estudio preliminar sobre la ictiogeografia del pais. Minist. Agric. Cria. Of. Nac. Pesca. Caracas, Venezuela, 283 p.

MATSUBARA, K.
1963. Fish morphology and hierarchy. Part 1. 2d ed. Ishizaki-Shoten, Tokyo, 789 p.

NAKAMURA, H.
1935. On the two species of the thresher shark from Formosan waters. Mem. Fac. Sci. Agric. Taihoku Imp. Univ. 14:1-6.

OKADA, Y., M. AOKI, Y. SATO, AND H. MASAI.
1969. The brain patterns of sharks in relation to habit. J. Hirnforsch. 11:347-365.

OSIPOV, V. G.
1968. Some features of the distribution of tuna and other pelagic fishes in the northwestern Indian Ocean. (Nekotorye osobennoste raspredeleneya Tunstov i drugekh pelagechekikh ryb v severo-zapadnoii chasti Indiiskogo Okena.) (Transl. in Probl. Ichthyol. 8:22-28.)

RAFINESQUE, C. S.
1809. Caratteri di alcuni nuovi generi e nuovi specie di animali e piante della Sicilia. Sanfilippo, Palermo, 105 p.

RIDEWOOD, W. G.
1921. On the calcification of the vertebral centra in sharks and rays. Philos. Trans. R. Soc. Lond., Ser. B, Biol. Sci. 210:311-407.

SADOWSKI, V., AND A. F. DE AMORIM.
1977. Sobre a composicao de fauna dos esqualos pelagicos do Brasil. Cienc. Cult., Supl. Resumos 29(7):792.

SALVIANI, I.
1554. Aquatiluim animalium historiae Liber Primus, cum eorumdem Formis, Aere Excuis. Romae Medicinam Profitente Auctore, Romae, 256 p.

SCHWARTZ, F. J., AND G. H. BURGESS.
1975. Sharks of North Carolina and adjacent waters. N.C. Dep. Nat. Econ. Resour., 57 p.

SPRINGER, S.
1943. A second species of thresher shark from Florida. Copeia 1943:54-55.
1960. Natural history of the sandbar shark, *Eulamia milberti*. U.S. Fish Wildl. Serv., Fish. Bull. 61:1-38.
1961. Dynamics of the feeding mechanism of large galeoid sharks. Am. Zool. 1:183-185.
1963. Large sharks of the Florida-Caribbean region. *In* P. W. Gilbert (editor), Sharks and survival, p. 96-124. D.C. Heath Co., Boston.
1966. A review of the western Atlantic cat sharks Scyliorhinidae, with descriptions of a new genus and five new species. U.S. Fish Wildl. Serv., Fish. Bull. 65:581-624.

SPRINGER, V. G.
1964. A revision of the carcharhinid shark genera *Scoliodon*, *Loxodon*, and *Rhizoprionodon*. Proc. U.S. Natl. Mus. 115:559-632.

SPRINGER, V. G., AND J. A. GARRICK.
1964. A survey of vertebral numbers in sharks. Proc. U.S. Natl. Mus. 116:73-96.

STEVENS, J. D.
1975. Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L.). J. Mar. Biol. Assoc. U.K. 55:657-685.

STILLWELL, C. D., AND J. G. CASEY.
1976. Observations on the bigeye thresher shark, *Alopias superciliosus*, in the western North Atlantic. Fish. Bull., U.S. 74:221-225.

STRASBURG, D. W.
1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 58:335-361.

TANAKA, S., AND K. MIZUE.
1979. Studies on sharks—XV Age and growth of Japanese dogfish *Mustelus manazo* Bleeker in the east China Sea. Bull. Jpn. Soc. Sci. Fish. 45:43-50.

TELLES, A. M.
1970. Presence de *Alopias superciliosus* (Lowe) dans les mers du Portugal. Remarques sur les *Alopias* (Selachii) recents et fossiles. Arq. Mus. Bocage 11(19):363-378.

TENG, C. Y.
1962. Classification and distribution of the Chondrichthys of Taiwan. Privately published, Taipei, Taiwan, 304 p.

TORTONESE, E.
1938. Intorno agli squali del genere *Alopias*. Boll. Mus. Zool. Anat. Comp. Univ. Torino 46-III(78):1-7.

WASS, R. C.
1973. Size, growth, and reproduction of the sandbar shark, *Carcharhinus milberti*, in Hawaii. Pac. Sci. 27:305-318.

WHITE, E. G.
1937. Interrelationships of the elasmobranchs with a key to the order Galea. Bull. Am. Mus. Nat. Hist. 74(2):25-138.

WILLIAMS, F.
1968. Report on the Guinean Trawling Survey, Volume 1. Gen. Rep. Organ. Afr. Unity, Sci., Tech. Res. Comm., 828 p.

IMPAIRMENT OF THE CHEMOSENSORY ANTENNULAR FLICKING RESPONSE IN THE DUNGENESS CRAB, *CANCER MAGISTER*, BY PETROLEUM HYDROCARBONS

WALTER H. PEARSON,[1] PETER C. SUGARMAN,[1] DANA L. WOODRUFF,[1] AND BORI L. OLLA[2]

ABSTRACT

After exposing Dungeness crabs in a continuous-flow system to seawater contaminated with Prudhoe Bay crude oil (0.27 parts per million), we observed the behavior of crabs presented with a clam extract. In response to seawater solutions of clam extract, Dungeness crabs change antennular orientation and increase antennular flicking rate. After 24-hour exposure and with oil still present, the proportion of crabs showing the changes in antennular behavior indicating detection of chemical food cues was significantly reduced. In contrast, the proportion showing chelae probing was not. Within 1 hour after return to clean water the antennular response recovered. Such rapid recovery indicates that the chemosensory impairment probably did not derive from structural damage to sensory cells but does not indicate which of several other possibilities was the most likely mechanism. By impairing the chemosensory antennular flicking response of Dungeness crabs, petroleum hydrocarbons could cause crabs some difficulty in finding food.

For marine organisms, disruption of chemoreception by oil is viewed as both likely and of important ecological consequence (Blumer 1969; Olla et al. 1980). Chemosensory disruption by various petroleum hydrocarbons and oil fractions has been reported in snails (Jacobson and Boylan 1973; Hyland and Miller 1979), lobsters (Atema and Stein 1974), and in shore crabs (Takahashi and Kittredge 1973). In some of these early studies the exposure regime was not well defined and did not always compare well with the length and level of exposure likely to be encountered in oil spills. Here we report on the ability of the Dungeness crab, *Cancer magister* Dana, to detect and respond to a food extract after 24-h exposure to seawater contaminated with Prudhoe Bay crude oil in a continuously flowing seawater system.

The antennules of many decapod crustaceans are a site for chemoreception of water-borne chemical cues (Hazlett 1971a). Antennular flicking may be analogous to sniffing in vertebrates (Fuzessery 1978) and enhances the ability of crustaceans to detect changes in their chemical environment (Schmitt and Ache 1979). Behavioral observations of antennular flicking rate indicate that detection of a clam extract occurs at 10^{-15} g/l in the blue crab, *Callinectes sapidus* (Pearson and Olla 1977), and at 10^{-10} g/l in the Dungeness crab (Pearson et al. 1979).

To determine whether exposure to petroleum hydrocarbons impaired this acute detection ability, we exposed Dungeness crabs to oil-contaminated seawater for 24 h, presented them with a clam extract in the presence of the oil-contaminated seawater, and recorded the percentages of crabs showing the changes in antennular behavior indicative of detection and of those showing the chelae probing indicative of food searching. At 24 h and 48 h after stopping the flow of oil-contaminated seawater, we retested the crabs to determine the time necessary for recovery of detection ability. Because this first experiment indicated rapid recovery, we performed a similar second experiment in which we presented the clam extract to Dungeness crabs 1 h after stopping the flow of contaminated seawater.

MATERIALS AND METHODS

Animal Collection and Maintenance

Dungeness crabs trapped in the Strait of Juan de Fuca, Wash., were held under the conditions described by Pearson et al. (1979). Seawater temperatures during the two experiments were 8.9 (±2.7 SD)° C (n = 16) and 9.2 (±0.5)° C (n =

[1]Battelle Pacific Northwest Laboratories, Marine Research Laboratory, Washington Harbor Road, Sequim, WA 98382.
[2]Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732.

Manuscript accepted June 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

16); salinities, 31.8 (±0.4)‰ (n = 5) and 32.0 (±0.0)‰ (n = 4); and dissolved oxygen 7.6 (±0.7) mg/l (n = 16) and 8.0 (±0.3) mg/l (n = 9). Clumps of the blue mussel, *Mytilus edulis*, and the littleneck clam, *Protothaca staminea*, provided an ad libitum diet.

Experimental Apparatus

We coupled the oil delivery system developed by Vanderhorst et al. (1977), and used extensively by Anderson et al. (1979, 1980), to the chemosensory testing apparatus of Pearson et al. (1979). Seawater contaminated with Prudhoe Bay crude oil was delivered to 20 of the 40 chemosensory testing chambers from dripper arms situated along manifolds connected to the oil delivery system. Contaminated water entered each exposure chamber at 0.1 l/min while clean water entered at 0.9 l/min. Control chambers received clean water at 1.0 l/min. Seawater entered each chamber through a glass funnel connected to a slotted inlet tube within the chamber. Teflon[3] tubes carried seawater solutions of the clam extract to the funnels from burets calibrated to deliver 20 ml within 15 s. Previous dye studies of Pearson et al. (1979) showed that the maximum concentration of an introduced solution within a chamber occurs 10 s after introduction and is 0.011 (±0.003) times the concentration of the introduced solution.

The delivery system produced oil-contaminated seawater that was largely a water-soluble fraction with some finely dispersed droplets. The chemical composition of this oil-contaminated seawater has been well characterized by Bean et al. (1978) and reported by Anderson et al. (1980). Here we sampled seawater in the testing chambers by the resin column absorption technique of Bean et al. (1978) and analyzed the samples by infrared (IR) spectrophotometry. The data of Bean et al. and Anderson et al. show the correlations between the values determined by IR and the concentration of specific hydrocarbons determined by other methods for the same system. To determine how rapidly hydrocarbon concentrations dropped after stopping the flow of oil-contaminated water in the second experiment, we supplemented IR analyses with analyses for monoaromatic hydrocarbons by a helium gas partitioning technique modified from McAuliffe (1971).

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Experimental Solutions

The experimental solutions were seawater solutions of freeze-dried clam extract (FDCE) of littleneck clam prepared following Pearson et al. (1979). Stock solutions averaging 1.89 (±0.12) g FDCE/l (n = 6) for the first experiment and 2.06 (±0.22) g FDCE/l (n = 5) for the second were refrigerated and used within 5 d. A 10^{-6} dilution of the stock FDCE solution was made 1 h before testing with seawater freshly filtered through a 0.4 μm membrane. An aliquot of the filtered seawater used for dilution was used as the control solution. All solutions were held in a water bath at ambient seawater temperature.

Procedures

After the oil delivery system had been operating for several days and the hydrocarbon concentrations measured, a single Dungeness crab was added to each of the 20 exposure and 20 control chambers. Chemosensory testing was synchronized to begin and end within either a rising or falling tide and after 24-h exposure to oil-contaminated seawater. In the first experiment, the FDCE solutions were presented with oil-contaminated seawater still flowing through the chambers. Each crab was presented with either one of two dilutions of FDCE or a control of filtered seawater. After correction for dilution within a chamber, these FDCE concentrations were 10^{-2} and 10^{-8} g/l. The choice of dilution and the order of presentation were randomized except that active crabs and those with retracted antennules were passed over. The observer did not know the identity of any solution. An individual crab was observed for 60 s prior to introduction of experimental solution, and the antennular flicking rate and other behavior recorded. The observer depressed a switch of an event counter for each flick of one antennule. The solution (20 ml) was then introduced and observation continued for another 60 s from onset of introduction.

The criteria of Pearson et al. (1979) were used to score the behavior. Detection was indicated when a crab abruptly changed antennular orientation and increased antennular flicking rate so that the ratio of the rate after solution introduction to that before was 1.50 or higher. Previous observations indicate that the a priori probability that such an increase in antennular flicking is spontaneous, rather than in response to the solution, is $<5\%$

(Pearson et al. 1979). The onset of food searching was indicated when a crab probed the substrate with its chelae or exhibited the capture response described by Pearson et al. (1979).

To examine recovery of detection ability, we stopped the flow of oil-contaminated water after the first presentation of FDCE. Clean seawater then entered the chambers at 0.9 l/min. After 24 h and 48 h both exposed and control crabs were again presented with experimental solutions and their behavior observed and scored.

Because the first experiment indicated rapid recovery, we wished to see if such recovery was quick as 1 h and, therefore, repeated the exposure phase of the first experiment. Instead of presenting FDCE with oil-contaminated water still present, we turned off the contaminated water and presented the FDCE 1 h later. The start and finish of exposure for individual crabs was staggered to achieve this 1-h clearance of oil from the chambers.

Statistical Analysis

The experiments were run until 28-33 crabs had been tested under each experimental condition. The numbers of crabs detecting and not detecting the various experimental solutions were totaled for exposed and control conditions. Although data is presented as the percentage of crabs detecting the FDCE, chi-square analysis was done on 2×2 contingency tables of the number of crabs detecting or not detecting under control or exposed conditions. Data for crabs showing chelae probing were treated similarly.

RESULTS

Hydrocarbon Concentrations

During the first experiment, where the clam extract was presented in the presence of oil-contaminated seawater, the total hydrocarbon concentrations by IR analyses were 0.27 ($\pm$0.04) ppm (n = 22) during the 24-h exposure and 0.013 ($\pm$0.004) ppm (n = 6) 24 h after the oil-contaminated water was stopped. During the second experiment, where the clam extract was presented 1 h after stopping the oil-contaminated seawater, the total hydrocarbon concentration by IR averaged 0.34 ($\pm$0.07) ppm (n = 10). Also, in the second experiment after 1 h the concentration of monoaromatic hydrocarbons (Table 1) fell to 0.008 times the exposure level.

TABLE 1.—The concentrations (parts per billion) of monoaromatic hydrocarbons in the testing chambers. Determined by helium gas partitioning, n = 4.

	Hydrocarbon concentrations			
	During 24 h of continuous flow		1 h after flow stopped	
Hydrocarbon	$\bar{x}$	SD	$\bar{x}$	SD
Benzene	50.1	10.8	0.13	0.24
Toluene	85.0	12.7	.16	.31
Ethylbenzene	13.8	2.8	.74	.95
m- plus *p*-Xylene	38.0	5.2	.94	1.36
o-Xylene	19.5	3.4	.90	1.22
Total trimethylbenzenes	40.6	11.9	<.01	
Total	247.0	34.7	1.98	3.76

Impairment and Recovery of Chemosensory Detection

After 24-h exposure to and still in the presence of oil-contaminated seawater, the percentage of exposed crabs detecting the clam extract was about half that of control crabs (Table 2). In contrast, the percentage of crabs probing with chelae did not differ significantly between control and exposed conditions (Table 3). Of the exposed crabs that probed the substrate with their chelae after presentation of 10^{-2} g FDCE/l, 48% (n = 25) did so without the normally preceding increase in the antennular flicking rate to above the criterion ratio of 1.50. One control crab (3%, n = 31) probed with the chelae without the normal increase in the antennular flicking rate. For crabs showing chelae probing, the antennular flicking rate ratio was significantly higher for control individuals (median = 2.36, range = 1.46-17.50, n = 31) than for exposed individuals (median = 1.56, range = 0.76-6.82, n = 25; median test, χ^2 = 9.19, df = 1, P = 0.998). Previously, no Dungeness crab (n = 89) presented with high levels of clam extract (10^{-3} to 10^{-6} g/l) showed chelae probing without first increasing the antennular flicking rate (Pearson et al. 1979).

Recovery of detection ability occurred rapidly. In the first experiment the percentage of crabs detecting FDCE at both levels did not differ between control and exposed conditions for both 24 h and 48 h (Table 2). In the second experiment, where the FDCE was presented 1 h after the flow of oil-contaminated seawater was stopped, again the percentage of crabs detecting did not differ significantly between control and exposed conditions (Table 4).

Whereas the antennular response to the clam extract was reduced under exposure and recovered after return to clean water, the basic rate of

TABLE 2.—Percentage of Dungeness crabs detecting the clam extract (FDCE) after exposure to continuously flowing seawater contaminated with Prudhoe Bay crude oil.

FDCE (g/l)	Treatment	After 24-h exposure				After 24 h in clean water				After 48 h in clean water			
		No. tested	Detecting (%)	χ^2	P	No. tested	Detecting (%)	χ^2	P	No. tested	Detecting (%)	χ^2	P
10^{-2}	Control	32	97	16.0	0.999	37	95	1.18	0.723	31	97	1.96	0.838
	Exposed	30	53			31	87			31	87		
10^{-8}	Control	34	32	3.46	.937	38	42	.05	.177	31	36	1.06	.697
	Exposed	31	13			33	39			31	48		
Control	Control	18	17	.40	.473	17	35	.13	.282	16	40	1.97	.840
	Exposed	20	25			22	41			17	18		

TABLE 3.—Percentage of Dungeness crabs probing with the chelae upon presentation of a clam extract (FDCE) after exposure to continuously flowing seawater contaminated with Prudhoe Bay crude oil.

FDCE (g/l)	Treatment	After 24-h exposure				After 24 h in clean water				After 48 h in clean water			
		No. tested	Probing (%)	χ^2	P	No. tested	Probing (%)	χ^2	P	No. tested	Probing (%)	χ^2	P
10^{-2}	Control	32	97	2.18	0.860	37	84	0.114	0.265	31	84	2.20	0.862
	Exposed	30	87			31	81			31	68		
10^{-8}	Control	34	6	.329	.434	38	5	.395	.470	31	0	1.02	.687
	Exposed	31	10			33	9			31	3		
Control	Control	18	0	.924	.664	17	0	.793	.627	16	6	1.10	.705
	Exposed	20	5			22	4			17	0		

TABLE 4.—Percentage of Dungeness crabs responding to a clam extract (FDCE) presented in clean water 1 h after 24-h exposure to oil-contaminated seawater.

FDCE (g/l)	Treatment	No. tested	Crabs detecting			Crabs chelae probing		
			%	χ^2	P	%	χ^2	P
10^{-2}	Control	28	96	0.002	0.040	89	0.952	0.671
	Exposed	30	97			80		
10^{-8}	Control	33	42	.551	.542	0	1.118	.710
	Exposed	30	33			3		
Control	Control	19	37	.681	.591	0		
	Exposed	13	23			0		

antennular flicking was not affected by exposure. The antennular flicking rate during the minute before introduction of the clam extract did not vary under exposure, control or recovery conditions over both experiments (median test, $\chi^2 = 2.62$, df = 7, $P = 0.08$). The overall grand median flicking rate was 33 flicks/min ($n = 653$). The median antennular flicking rate for resting Dungeness crabs was previously found to be 30 flicks/min (Pearson et al. 1979).

DISCUSSION

Whereas our exposure regime was low, brief, and well-characterized compared with most of the oil effects studies to date, we must clarify the circumstances to which our exposure is applicable. We exposed Dungeness crabs for 24 h to oil-contaminated seawater (0.27 ppm total hydrocarbons by IR) in which dissolved monoaromatic hydrocarbons (0.247 ppm) predominated. Our system produced this oil-contaminated seawater by continuous mixing of fresh oil with flowing seawater (9° C) followed by separation of floating oil and diversion of nonfloating mixture to the exposure chambers (Vanderhorst et al. 1977).

For a study of its kind we believe our exposure regime to be the best characterized to date, but the exposure regime is not representative of all, or perhaps even most, oil spill situations. Concentrations of total oil in the water ranging from 0.1 to 1.0 and lasting several days have indeed been reported (Grahl-Nielsen 1978; Calder and Boehm in press), but in such cases detection of substantial amounts of alkane (saturate) hydrocarbons indicated that an unknown but substantial amount of oil was emulsified, i.e., present as droplets. Because only 2% of the total hydrocarbons in our oil-contaminated seawater were saturates (Anderson et al. 1980), our exposure regime did not mimic situations where emulsified oil and high proportions of saturate hydrocarbons exist. The chemosensory effects of emulsified oil remain to be studied. Our results are most applicable to situations where dissolved monoaromatic hydrocarbons predominate in the water column.

When oil is spilled, monoaromatic hydrocarbons usually do not attain high concentrations in the water column but rather are rapidly lost by evaporation (McAuliffe 1977a, b). During the last 3 d of a 21-d platform spill in the Gulf of Mexico McAuliffe et al. (1975) measured total low molecular weight (C_1-C_9) hydrocarbons in the water column using a gas equilibration method similar

to ours and found concentrations ranging from 0.002 to 0.010 ppm at 5 and 10 m. Near-surface concentrations ranged from a maximum of 0.200 ppm near the platform (230 m) to 0.002 ppm at a distance (1.5 km). About half these C_1-C_9 hydrocarbons, i.e., 0.100 ppm, were the monoaromatics predominating in our oil-contaminated seawater. During four 10.5-barrel experimental spills concentrations of C_2-C_{10} aromatic hydrocarbons ranged from 0.002 to 0.050 ppm at 1.5 m within 20 min after the spill and were not detectable after 1 h (McAuliffe 1977b). Because the low temperature (9° C) of our seawater and perhaps other system properties slow evaporative loss, our system produced oil-contaminated seawater with a monoaromatic concentration 2.5 to 5 times higher than those reported in the water column during spills. While our higher concentration has not been reported, it is conceivable that subsurface leakage of fresh oil from pipelines or sunken vessels into cold water could produce exposures similar to ours.

One example of how cold temperature and other hydrographic conditions may combine to prevent evaporative loss and allow monoaromatic concentrations more persistent and higher than those cited above for oil spills is found in Valdez Arm, Alaska. Because of the stratification of the water column typical of a fjord, effluent from the oil tanker ballast water treatment facility at Valdez does not mix uniformly but instead is confined to a lens near the bottom. The treatment facility releases about 4.5×10^7 l (12×10^6 gal) daily (Lysyj et al. 1979) with average concentrations of monoaromatic hydrocarbons between 5.1 and 6.4 ppm (Lysyj et al. 1979, 1981; Rice et al. 1981). The distribution of monoaromatics in the receiving body was studied by Lysyj et al. (1981) who found the monoaromatics trapped within a narrow (10 m) zone of maximum concentration that spread horizontally 2 to 3 km in a thin pancake shape. Depth of the pancake varied with season from 50 to 65 m and approached the bottom. A monoaromatic concentration of 0.021 ppm was found 2 m off the bottom, and the maximum monoaromatic concentration observed was 0.127 ppm, half of the exposure concentration used here. Our exposure regime then may be most applicable to situations where there is chronic release of monoaromatic hydrocarbons under hydrographic conditions, e.g., low temperatures and stratification of the water column, that prevent evaporative loss.

The observed chemosensory impairment under oil exposure could have derived from several possible mechanisms, structural damage to chemoreceptor cells, anesthesia of chemoreceptors or other neurons, masking of food cue odor by oil, oil-induced changes in motivation, or coating or matting of the sensory hairs of the antennule by oil. The rapid recovery of the antennular flicking response eliminates only direct structural damage to the chemoreceptor cells as a possibility. Cellular damage would have required a recovery period of days whereas other mechanisms, such as masking or anesthesia, would have been rapidly reversible upon return to clean seawater (Johnson 1977). Anesthesia of the chemoreceptor or higher level neurons remains possible because our oil-contaminated seawater contained several aromatic and saturate hydrocarbons known to produce anesthesia or reversible narcosis in barnacle larvae (Crisp et al. 1967). Dungeness crabs do detect the water-soluble fraction of Prudhoe Bay crude oil at 10^{-4} ppm (Pearson et al. 1980) so that masking of the clam extract by the odor of oil was also possible. Odor masking by oil was also suggested by Atema and Stein (1974) as one possible mechanism behind a longer food finding time in the northern lobster, *Homarus americanus*. A change in feeding motivation was also suggested by Atema and Stein, but the observation in our first experiment of no difference between exposed and control conditions in the proportion of Dungeness crabs showing the chelae probing indicative of food searching argues against a change in motivation having occurred here. Antennular flicking enhances the ability of crustaceans to detect changes in the chemical milieu by splaying out the sensory hairs and increasing the passage of stimulative chemicals to the sensory neurons (Schmitt and Ache 1979), and oil might impair chemosensory function by slowing the passage of stimulating chemicals through coating or matting of the sensory hairs. Because our system produced oil-contaminated seawater with only 2% saturate hydrocarbons (Anderson et al. 1980) and thus little oil existed as emulsified droplets rather than dissolved hydrocarbons, we feel that in our system coating of the sensory hairs was not as likely as one of the other mechanisms. In a spill like the *Amoco Cadiz* where large amounts of oil are emulsified by turbulence (Calder and Boehm in press) physical blockage of chemical cues by the coating of sensory hairs is a possibility that needs study. Whereas

our behavioral results indicate direct structural damage to chemosensory cells was unlikely, which of the other mechanisms actually produced the observed chemosensory impairment remains an open question.

Decapod crustaceans have two chemoreceptor systems, one seated in the antennules and another in the dactyls, chelae, and mouth parts (Luther 1930; Case and Gwilliam 1961; Levandowsky and Hodgson 1965; Hazlett 1968, 1971a, b). The observation that after presentation with a clam extract a significant proportion of exposed crabs showed chelae probing without the normally preceding increase in antennular flicking suggests that 24-h exposure to our oil-contaminated seawater depressed the functioning of the antennular system in Dungeness crabs while, at least as far as we can determine, not significantly affecting the dactyl chemoreceptor system. Perhaps longer exposure would have affected the dactyl system.

The practical implication that needs further investigation is how the observed impairment of the chemosensory antennular flicking response would affect food foraging by the Dungeness crab. Whereas the exact role of the antennules in food finding is not fully understood, abundant evidence exists for the involvement of the antennules in food searching. Upon water-borne chemical stimulation, increases in antennular flicking rate precede food searching behaviors in the Dungeness crab (Pearson et al. 1979) and the blue crab (Pearson and Olla 1977). Because the electrophysiological work of Schmitt and Ache (1979) demonstrated that antennular flicking enhances perception of changes in the chemical milieu, increased flicking would presumably further enhance detection of rapid chemical changes. In the spiny lobster, *Panulirus argus*, chemical stimulation of the antennules usually initiated feeding behavior although chemical-tactile stimulation of the dactyl was more effective (Maynard and Sallee 1970). In hermit crabs intact antennules were necessary to sustain feeding behavior when contact with food is not direct and immediate (Hazlett 1968). Ablation of the antennules impaired the ability of the pelagic shrimp, *Acetes sibogae australis*, to follow food scent trails although antennular ablation did not prevent the detection of scent trails (Hamner and Hamner 1977). The ablation experiments of Reeder and Ache (1980) showed that chemosensory input from the lateral aesthetasc hair tufts of the antennules triggers food searching by *P. argus* and guides the spiny lobster to a distant odor source. Our observation of an impaired chemosensory antennular flicking response coupled with the good evidence of antennular involvement in food finding indicated that difficulty in finding food in the presence of petroleum hydrocarbons is a possibility for Dungeness crabs. If the antennular chemoreceptor system is as critical to successful guidance to distant odor sources in the Dungeness crab as the results of Reeder and Ache (1980) showed it is for the spiny lobster, then we particularly need to investigate whether entry to baited traps is affected when dissolved aromatic or other hydrocarbons are present.

ACKNOWLEDGMENTS

This work was supported by the National Oceanic and Atmospheric Administration of the U.S. Department of Commerce under the Interagency Energy-Environment Program of the U.S. Environmental Protection Agency.

We thank J. W. Anderson for his valuable discussions. Chemical analyses were performed by J. W. Blaylock and J. Webster.

LITERATURE CITED

ANDERSON, J. W., S. L. KIESSER, AND J. W. BLAYLOCK.
1979. Comparative uptake of naphthalenes from water and oil sediment by benthic amphipods. *In* Proceedings of the 1979 Oil Spill Conference, p. 579-584. Am. Pet. Inst., Wash., D.C.
1980. The cumulative effect of petroleum hydrocarbons on marine crustaceans during constant exposure. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 179:62-70.

ATEMA, J., AND L. S. STEIN.
1974. Effects of crude oil on the feeding behaviour of the lobster *Homarus americanus*. Environ. Pollut. 6:77-86.

BEAN, R. M., J. W. BLAYLOCK, AND R. G. RILEY.
1978. Application of trace analytical techniques to a study of hydrocarbon composition upon dispersion of petroleum in a flowing seawater system. *In* Proceedings of a Symposium on Analytic Chemistry of Petroleum Hydrocarbons in the Marine Aquatic Environment, p. 902-908. Div. Pet. Chem., Am. Chem. Soc.

BLUMER, M.
1969. Oil pollution of the ocean. *In* D. P. Hoult (editor), Oil on the sea; proceedings of a symposium on the scientific and engineering aspects of oil pollution of the sea, p. 5-13. Plenum Press, N.Y.

CALDER, J. A., AND P. D. BOEHM.
In press. The chemistry of AMOCO CADIZ oil in the Aber Wrach. *In* AMOCO CADIZ Conséquences D'une Pollution Accidentelle Par Les Hydrocarbures, p. 149-158. Publiś Par Le Centre National Pour L'Exploitation Des Oceans, Paris.

CASE, J., AND G. F. GWILLIAM.
1961. Amino acid sensitivity of the dactyl chemoreceptors of *Carcinides maenas*. Biol. Bull. (Woods Hole) 121: 449-455.

CRISP, D. J., A. O. CHRISTIE, AND A. F. A. GHOBASHY.
1967. Narcotic and toxic action of organic compounds on barnacle larvae. Comp. Biochem. Physiol. 22:629-649.

FUZESSERY, Z. M.
1978. Quantitative stimulation of antennular chemoreceptors of the spiny lobster, *Panulirus argus*. Comp. Biochem. Physiol. 60:303-308.

GRAHL-NIELSON, O.
1978. The Ekofisk Bravo Blowout: petroleum hydrocarbons in the sea. *In* Proceedings of The Conference on Assessment of Ecological Impacts of Oil Spills, p. 477-487. Am. Inst. Biol. Sci., Arlington, Va.

HAMNER, P., AND W. M. HAMNER.
1977. Chemosensory tracking of scent trails by the planktonic shrimp *Acetes sibogae australis*. Science (Wash., D.C.) 195:886-888.

HAZLETT, B. A.
1968. Stimuli involved in the feeding behavior of the hermit crab *Clibanarius vittatus* (Decapoda, Paguridea). Crustaceana 15:305-311.
1971a. Antennule chemosensitivity in marine decapod crustacea. J. Anim. Morphol. Physiol. 18:1-10.
1971b. Chemical and chemotactic stimulation of feeding behavior in the hermit crab *Petrochirus diogenes*. Comp. Biochem. Physiol. 39A:665-670.

HYLAND, J. L., AND D. C. MILLER.
1979. Effects of No. 2 fuel oil on chemically-evoked feeding behavior of the mud snail, *Ilyanassa obsoleta*. *In* Proceedings of the 1979 Oil Spill Conference, p. 603-607. Am. Pet. Inst., Wash., D.C.

JACOBSON, S. M., AND D. B. BOYLAN.
1973. Effect of seawater soluble fraction of kerosene on chemotaxis in a marine snail, *Nassarius obsoleta*. Nature (Lond.) 241:213-215.

JOHNSON, F. G.
1977. Sublethal biological effects of petroleum hydrocarbon exposures: bacteria, algae, and invertebrates. *In* D. C. Malins (editor), Effects of petroleum on Arctic and Subarctic marine environments and organisms, Vol. II, p. 271-335. Acad. Press, N.Y.

LEVANDOWSKY, M., AND E. S. HODGSON.
1965. Amino acid and amine receptors of lobsters. Comp. Biochem. Physiol. 16:159-161.

LUTHER, W.
1930. Versuche über die chemorezeption der brachyuran. Z. vgl. Physiol. 12:177-205.

LYSYJ, I., R. RUSHWORTH, R. MELVOLD, AND J. FARLOW.
1979. Effectiveness of a large-scale ballast treatment process. *In* Proceedings of the 1979 Oil Spill Conference, p. 133-137. Am. Pet. Inst., Wash., D.C.

LYSYJ, I. G., G. PERKINS, J. S. FARLOW, AND R. M. MORRIS.
1981. Distribution of aromatic hydrocarbons in Port Valdez, Alaska. *In* Proceedings of the 1981 Oil Spill Conference, p. 47-53. Am. Pet. Inst., Wash., D.C.

MAYNARD, D. M., AND A. SALLEE.
1970. Disturbance of feeding behavior in the spiny lobster, *Panulirus argus*, following bilateral ablation of the *Medulla terminalis*. Z. vgl. Physiol. 66:123-140.

MCAULIFFE, C. D.
1971. GC determination of solvents by multiple phase equilibration. Chem. Technol. 1:46-51.
1977a. Dispersal and alteration of oil discharged on a water surface. *In* D. A. Wolfe (editor), Fate and effects of petroleum hydrocarbons in marine ecosystems and organisms, p. 19-35. Pergamon Press, Oxf.
1977b. Evaporation and solution of C_2 to C_{10} hydrocarbons from crude oils on the sea surface. *In* D. A. Wolfe (editor), Fate and effects of petroleum hydrocarbons in marine ecosystems and organisms, p. 363-372. Pergamon Press, Oxf.

MCAULIFFE, C. D., A. E. SMALLEY, R. D. GROOVER, W. M. WELSH, W. S. PICKLE, AND G. E. JONES.
1975. Chevron Main Pass block 41 oil spill: chemical and biological investigations. *In* Proceedings of the 1975 Joint Conference on Prevention and Control of Oil Spills, p. 555-556. Am. Pet. Inst., Wash., D.C.

OLLA, B. L., W. H. PEARSON, AND ANNE L. STUDHOLME.
1980. Applicability of behavioral measures in environmental stress assessment. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 179:162-173.

PEARSON, W. H., AND B. L. OLLA.
1977. Chemoreception in the blue crab, *Callinectes sapidus*. Biol. Bull. (Woods Hole) 153:346-354.

PEARSON, W. H., P. C. SUGARMAN, D. L. WOODRUFF, J. W. BLAYLOCK, AND B. L. OLLA.
1981. Detection of petroleum hydrocarbons by the Dungeness crab, *Cancer magister*. Fish. Bull., U.S. 78:821-826.

PEARSON, W. H., P. C. SUGARMAN, D. L. WOODRUFF, AND B. L. OLLA.
1979. Thresholds for detection and feeding behavior in the Dungeness crab, *Cancer magister* (Dana). J. Exp. Mar. Biol. Ecol. 39:65-78.

REEDER, P. B., AND B. W. ACHE.
1980. Chemotaxis in the Florida spiny lobster, *Panulirus argus*. Anim. Behav. 28:831-839.

RICE, S. D., S. KORN, C. C. BRODERSEN, S. A. LINDSAY, AND S. A. ANDREWS.
1981. Toxicity of ballast-water treatment effluent to marine organisms at Port Valdez, Alaska. *In* Proceedings of the 1981 Oil Spill Conference, p. 55-61. Am. Pet. Inst., Wash., D.C.

SCHMITT, B. C., AND B. W. ACHE.
1979. Olfaction: Responses of a decapod crustacean are enhanced by flicking. Science (Wash., D.C.) 205:204-206.

TAKAHASHI, F. T., AND J. S. KITTREDGE.
1973. Sublethal effects of the water soluble component of oil: Chemical communication in the marine environment. *In* D. G. Ahearn and S. P. Meyers (editors), The microbial degradation of oil pollutants, p. 259-264. La. State Univ. Press Publ. LSU-SG-73-01.

VANDERHORST, J. R., C. I. GIBSON, L. J. MOORE, AND P. WILKINSON.
1977. Continuous-flow apparatus for use in petroleum bioassay. Bull. Environ. Contam. Toxicol. 17:577-584.

REPRODUCTION, MOVEMENTS, AND POPULATION DYNAMICS OF THE SAND SEATROUT, *CYNOSCION ARENARIUS*[1,2]

PHILIP A. SHLOSSMAN AND MARK E. CHITTENDEN, JR.[3]

ABSTRACT

Cynoscion arenarius females mature at 140-180 mm total length as they approach age I. Spawning occurs from early March through September, but concentrates in a distinct spring period (March-May) and a distinct late summer period (August-September). Spawning occurs in the inshore Gulf of Mexico and coincides with the periodicity of onshore winds and surface currents which probably transport eggs or larvae to estuarine and inshore gulf nurseries. Estuarine nurseries may be most important to late summer spawned groups. The main gulf nursery in the northwestern area is in waters shallower than 18 m. Both spawned groups leave estuarine nurseries in fall to overwinter in the gulf. Late summer spawned groups return to estuaries in midspring but reenter the gulf in August to spawn. Fish average 210-280 mm total length at age I but some were 300 mm. Predicted sizes of late summer fish were 425 mm total length at age II and 574 mm at age III. The largest trawled specimen was 342 mm total length and 99.5% were less than 280 mm. No more than three spawned groups or two year classes occurred at any one time. The typical maximum life span is 1-2 years based on trawl data and possibly as much as 2-3 years for other gear. Total annual mortality rate was 99.79% based on trawling data and appears no lower than 80-90% if maximum lifespan typically is as great as 3 years. *Cynoscion arenarius* can be aged using scales. Total weight-total length, girth-total length, and standard length-total length regressions are presented. Temporal isolation of the two spawned groups produced each year suggests they may be separate populations or species. The life history and population dynamics of *C. arenarius* appear similar to *C. regalis* along the Atlantic coast south of Cape Hatteras, North Carolina. The latter taxon shows zoogeographic change at Cape Hatteras, which needs management consideration.

The sand seatrout, *Cynoscion arenarius* (Ginsburg), is endemic to the Gulf of Mexico (gulf) and ranges from southwest Florida (Roessler 1970) to the Bay of Campeche (Hildebrand 1955). It is one of the most abundant fishes in estuaries and the shallow gulf (Gunter 1945; Christmas and Waller 1973) and is a major component of the industrial fishery landings and shrimp bycatch (Roithmayr 1965; Gutherz et al. 1975).

The life history of *C. arenarius* is essentially undescribed despite its abundance. Food habits have been studied (Darnell 1958; Diener et al. 1974; Moffett et al. 1979), and general material appears in many faunal studies including Franks et al. (1972), Gallaway and Strawn (1974), and Chittenden and McEachran (1976). Much of this information is misleading, however, because the complex life history of this species has not been recognized. Literature on the possibly conspecific *C. regalis* might apply to *C. arenarius*, but their taxonomic status is still in doubt (Mohsin 1973; Weinstein and Yerger 1976). We have referred to *C. arenarius* herein as a species separate from *C. regalis* following Bailey et al. (1970).

This paper describes spawning seasonality, periodicity, and areas, seasonal distribution and movements, age determination, growth, mortality, and total weight-total length, girth-total length, and standard length-total length relations.

METHODS

Sand seatrout were collected monthly along a transect in the gulf off Freeport, Tex. (Figure 1), from October 1977 through September 1979 aboard a chartered shrimp trawler using twin 10.4 m (34-ft) trawls with a 4.4 cm stretched mesh cod end. Collections were made during the day through September 1978; thereafter, a day and a night cruise usually were made each month. Stations were occupied at depths of 4.5, 7, 9, 14-15, 18, 22, 27, 37, and 46 m. One or two tows were made at each depth (two tows after October 1978), except

[1]Based on a thesis submitted by the senior author in partial fulfillment of the requirements for the MS degree, Texas A&M University.

[2]Technical article TA 16254 from the Texas Agricultural Experiment Station.

[3]Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843.

Manuscript accepted June 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

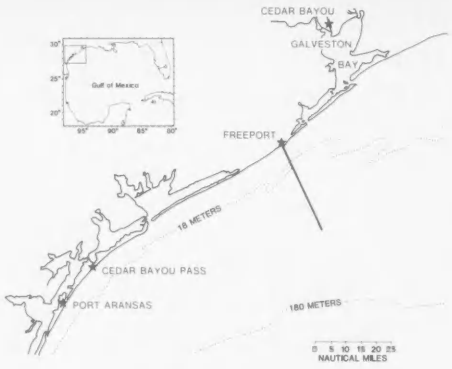

FIGURE 1.—Location of sampling area. Cedar Bayou Pass near Port Aransas is the study location of Simmons and Hoese (1959).

TABLE 1.—Description of gonad maturity stages assigned to *Cynoscion arenarius*.

Stage and name	Description
1 Immature	Gonads barely visible or not visible, sexes indistinguishable.
2 Maturing virgin	Gonads very small, sexes distinguished only with magnification.
3 Early developing	Sexes visually distinguished, ovaries occupy <25% of body cavity, individual eggs not visible to the naked eye.
4 Late developing	Ovaries occupy 25-50% of body cavity, eggs clearly visible to naked eye, no translucent eggs.
5 Gravid	Ovaries occupy at least 50% of body cavity, up to 50% of the eggs translucent.
6 Ripe	Ovaries occupy at least 50% of body cavity, >50% of the eggs translucent.
7 Spawning/spent	Ovaries flaccid and at least partly empty, no opaque eggs.
8 Resting	Ovaries fit same description as those in Stage 3, but fish are large enough and were collected at a time when they could already have spawned.

that 8-12 tows were made at 14-15 m and about 24 tows usually were made at 22 m. The 22 m depth primarily was occupied after October 1978.

Cynoscion spp. were culled from the catch, fixed in 10% Formalin,[4] and stored in 70% ethanol before analysis. *Cynoscion arenarius* was separated from *C. nothus* primarily by comparing the anal fin base to the eye width following DeVries (1979). Total length (TL) was measured on all fish. All specimens captured from October 1977 through December 1978, except as noted, were processed and scales were taken to determine age, standard length (SL), girth (G) at the anterior origin of the dorsal fin, total weight (TW), sex, ovary weight (GW) to the nearest 0.1 g, and gonad maturity stage. In June and early December 1978, 300 specimens were randomly selected except that all fish >120 mm TL were processed in June 1978. Scales were taken above the lateral line below the second dorsal fin following procedures for *C. regalis* (Perlmutter et al. 1956), and cellulose acetate impressions were examined using a scale projector. Females and immature fish were assigned gonad maturity stages (Table 1) slightly modified from Kesteven's system (Bagenal and Baum 1971).

Findings based on collections off Freeport were verified by the following materials. Fish were captured from February through December 1977 and in March, June, and July 1978 off Port Aransas, Tex., aboard the Texas Parks and Wildlife Department (TPWD) RV *Western Gulf* using a 13.7 m otter trawl with a 5.1 cm stretched mesh cod end. Stations usually were occupied at 11 m at night, at 7, 15, and 18-24 m during the day; and also at night at 20-22, 29-31, and 38 m from May through October 1977. Additional monthly day collections were made in Galveston Bay, Tex., aboard the TPWD RV *Drum II* from December 1977 through July 1979 using a 6 m otter trawl with a 3.8 cm stretched mesh cod end or a 3 m otter trawl with a 2.5 cm stretched mesh cod end. Finally, collections from July 1978 through July 1979 in Cedar Bayou, Tex., using a 3 m otter trawl with a 2.5 cm stretched mesh cod end were made available by Pridgeon.[5]

Spawned groups and their year class identities were indicated by specifying the season and year when they hatched, e.g., spring 1978. Spawning periodicities and group identities assume that a total length of 30 mm at 1 mo of age for *C. regalis* (Welsh and Breder 1923) applies to *C. arenarius*. Hatching dates of 1 April and 1 September were assigned to spring and late summer spawned groups to estimate growth and ages.

MATURATION AND SPAWNING PERIODICITY

Results

Cynoscion arenarius matures at 140-180 mm TL as they approach age I and spawn. Gonad devel-

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]B. Pridgeon, Graduate Research Assistant, Texas A&M University, College Station, TX 77843, pers. commun. December 1979.

opment was distinct at 140-200 mm TL as most specimens entered the early developing stage (Figure 2). Fish began to enter the late developing, gravid, or ripe stages at 180 mm TL. These data are supported by regressions of ovary weight on total length (Table 2, Figure 3) in which extrapolated x-intercepts were 120-170 mm TL in the March-September spawning period. Age compositions and sizes presented later indicate that *C. arenarius* matures to first spawn at 12 mo.

Sand seatrout spawn from early March through September. The collections off Freeport of fish 45-55 mm TL in mid-May 1978, 25-80 mm TL in mid-May 1979, and 60-120 mm TL in June and July of 1978 and 1979 (Figure 4) indicate that spawning began in early March and continued through May. This is supported by the collections of: 1) fish 50-75 mm TL off Port Aransas in late May and late June of 1977 and 1978 (Figure 5), 2) fish 50-80 mm TL in Galveston Bay in May 1978 and 1979 (Figure 6), and 3) fish 20-70 mm TL at Cedar Bayou in the period 1 May-2 July 1979 (Figure 7). Spawning also occurred in August and September; because a distinct group of fish 25-60 mm TL were collected off Freeport in late September 1979 (Figure 4), and fish 65-130 mm TL collected in early December of 1977 and 1978 were too small to represent spring spawning. This is supported by the collections of: 1) fish 25-50 mm TL at Cedar Bayou in September 1978 (Figure 7), 2) fish 70-120 mm TL in Galveston Bay in December 1977 and 50-80 mm TL in September-December 1978 (Figure 6), and 3) fish 70-150 mm TL off Port Aransas in February and December 1977 (Figure 5). Spawning did not occur from October through February, because no fish 25-60 mm TL were collected from November through April in the gulf (Figures 4, 5), in Galveston Bay (Figure 6), or at Cedar Bayou (Figure 7).

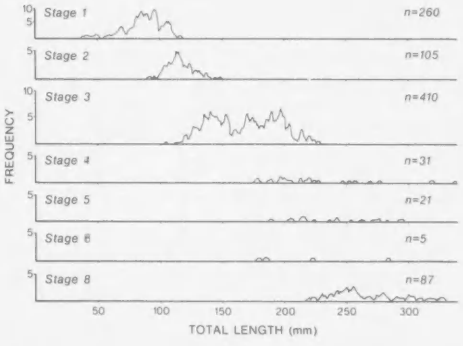

FIGURE 2.—Length frequencies (moving averages of three) of immature and female *Cynoscion arenarius* in maturity stages 1 through 8. Maturity stages are described in Table 1. No stage 7 fish were caught.

TABLE 2.—Analysis for regressions of gonad weight (grams) on total length (millimeters) for female *Cynoscion arenarius* each month, October 1977-December 1978. All regressions are significant at $\alpha = 0.05$.

Date	n	r^2	Equation
October 1977	75	0.759	$GW = -2.4537 + 0.0139\,TL$
November 1977	66	.801	$GW = -1.9946 + .0117\,TL$
December 1977	56	.828	$GW = -1.7127 + .0113\,TL$
February 1978	12	.353	$GW = -4.9977 + .0330\,TL$
March 1978	152	.503	$GW = -6.4522 + .0479\,TL$
April 1978	16	.702	$GW = -13.4576 + .0896\,TL$
May 1978	14	.579	$GW = -27.0498 + .1592\,TL$
June 1978	8	.696	$GW = -4.8433 + .0423\,TL$
July 1978	84	.436	$GW = -1.2198 + .0106\,TL$
September 1978	100	.498	$GW = -3.7836 + .0252\,TL$
October 1978	21	.250	$GW = -1.8382 + .0110\,TL$
December 1978	45	.673	$GW = -1.1223 + .0079\,TL$

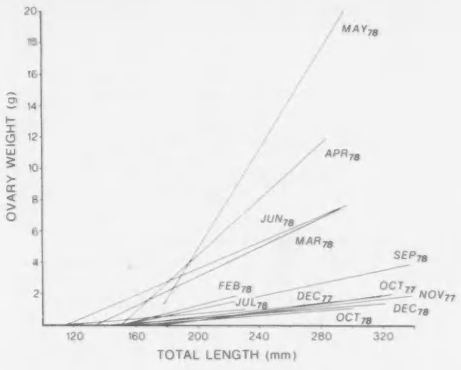

FIGURE 3.—Monthly ovary weight-total length regressions for *Cynoscion arenarius*. The length of each line shows the observed size range. X-intercepts indicate total length at which gonad development begins in what would be a curvilinear regression if smaller lengths were available.

Gonad maturity and weight data suggest that females spawned from February or March through September in agreement with length frequencies. Two gravid females were collected in mid-February 1978 and late developing, gravid, or ripe stage fish from March through July 1978 and in September 1978 (Figure 8). No spawning occurred from October through December, because all fish then were in resting, maturing virgin, or early developing stages. Gonad size increased during February (Figure 3), reached a peak in April and May, and rapidly declined through July. Increased

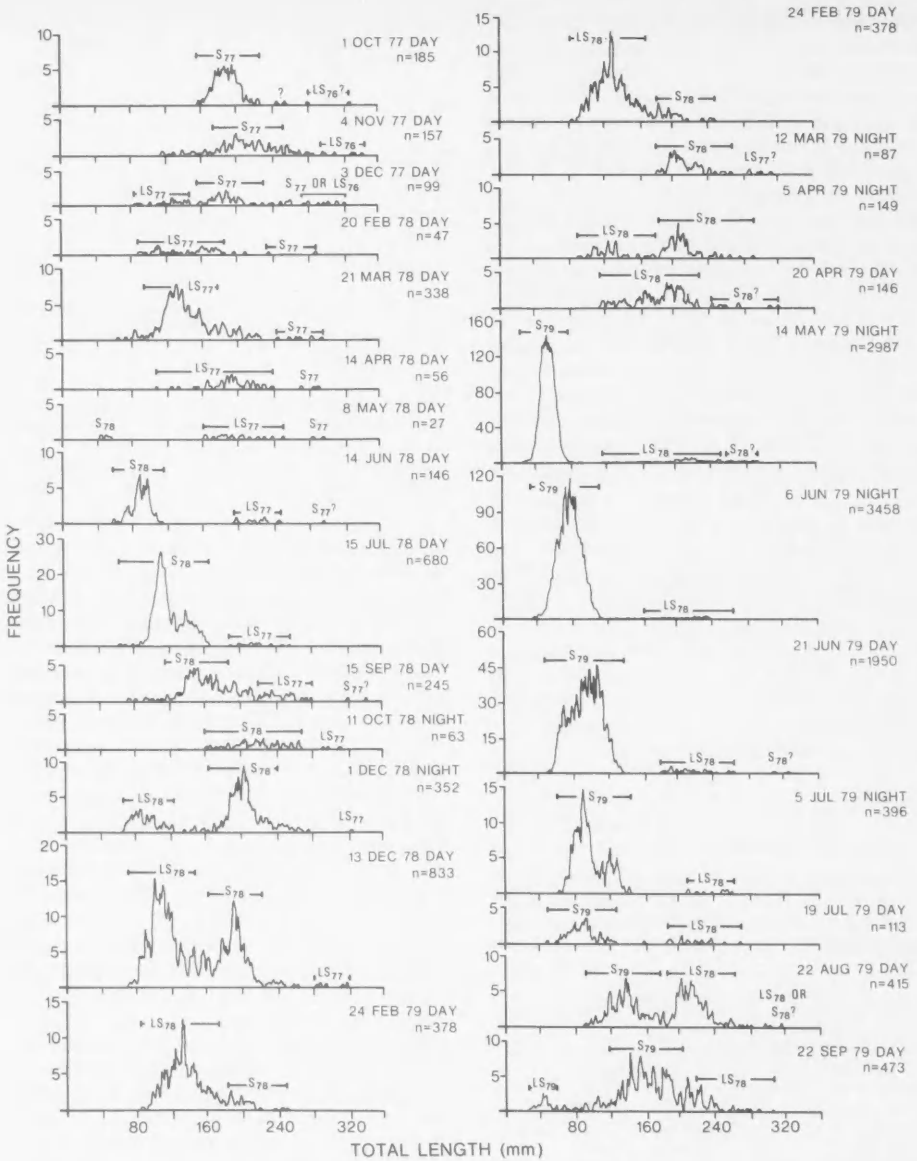
1 OCT 77 DAY n=185
4 NOV 77 DAY n=157
3 DEC 77 DAY n=99
20 FEB 78 DAY n=47
21 MAR 78 DAY n=338
14 APR 78 DAY n=56
8 MAY 78 DAY n=27
14 JUN 78 DAY n=146
15 JUL 78 DAY n=680
15 SEP 78 DAY n=245
11 OCT 78 NIGHT n=63
1 DEC 78 NIGHT n=352
13 DEC 78 DAY n=833
24 FEB 79 DAY n=378
12 MAR 79 NIGHT n=87
5 APR 79 NIGHT n=149
20 APR 79 DAY n=146
14 MAY 79 NIGHT n=2987
6 JUN 79 NIGHT n=3458
21 JUN 79 DAY n=1950
5 JUL 79 NIGHT n=396
19 JUL 79 DAY n=113
22 AUG 79 DAY n=415
22 SEP 79 DAY n=473
FREQUENCY
TOTAL LENGTH (mm)

FIGURE 4.—Monthly length frequencies (moving averages of three) of *Cynoscion arenarius* captured off Freeport, Tex. Spawned group identity (S = spring; LS = late summer) is often not clear where spawned groups meet.

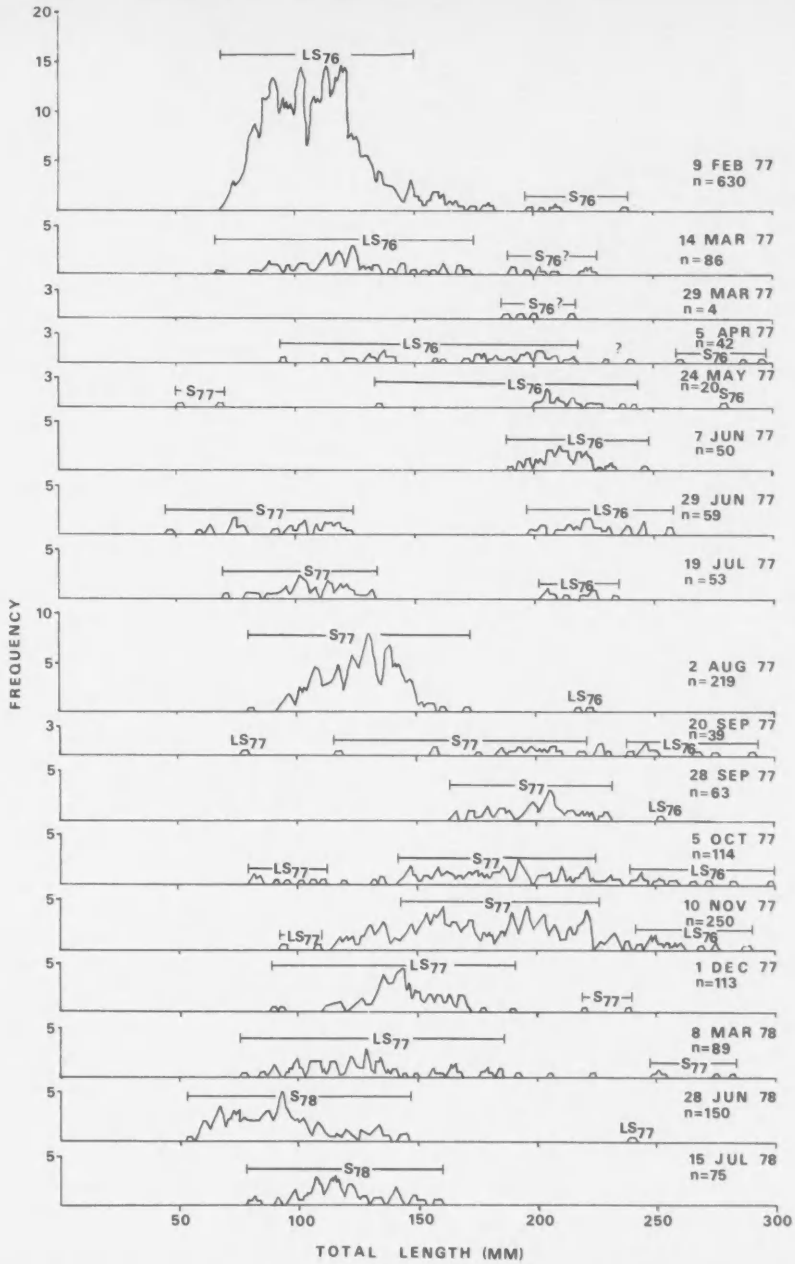

FIGURE 5.—Monthly length frequencies (moving averages of three) of *Cynoscion arenarius* captured off Port Aransas, Tex. Spawned group identity (S = spring; LS = late summer) is often not clear where spawned groups meet.

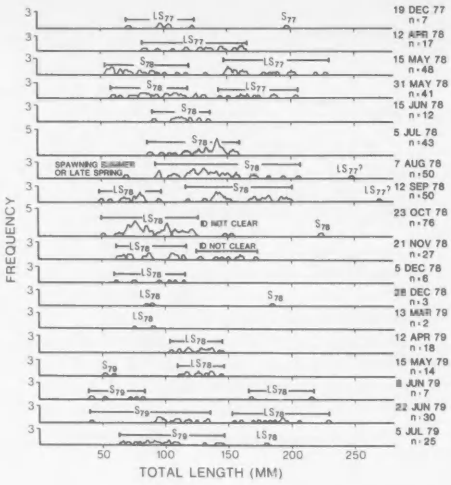

FIGURE 6.—Monthly length frequencies (moving averages of three) of *Cynoscion arenarius* captured in Galveston Bay, Tex. Spawned group identity (S = spring; LS = late summer; ID = identity) is often not clear where spawned groups meet. No fish were captured in February and March 1978 and February 1979.

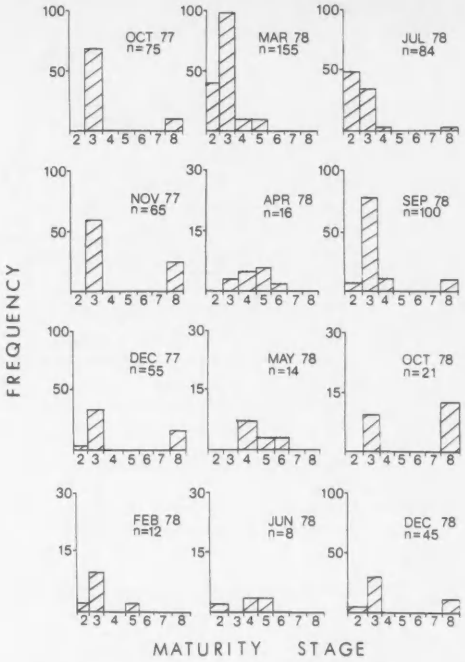

FIGURE 8.—Monthly maturity stages of female *Cynoscion arenarius*. Maturity stages are described in Table 1.

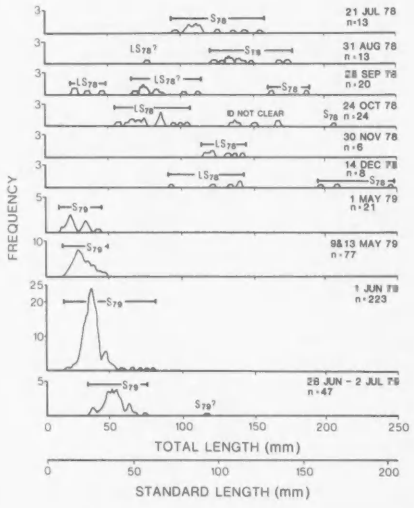

FIGURE 7.—Monthly length frequencies (moving averages of three) of *Cynoscion arenarius* captured in Cedar Bayou, Tex. Spawned group identity (S = spring; LS = late summer; ID = identity) is often not clear where spawned groups meet. No fish were captured from January through April 1979.

gonad size in mid-September might reflect August-early September spawning.

Although *C. arenarius* spawns over a broad time period, spawning primarily occurs during two discrete periods, a spring spawn from early March through May and a late summer spawn in August and September. Spring spawned fish formed length-frequency modes readily followed in the periods: 1) May-December 1978 and May-September 1979 off Freeport (Figure 4), 2) May-September 1977 and June-July 1978 off Port Aransas (Figure 5), 3) May-September 1978 and May-July 1979 in Galveston Bay (Figure 6), and 4) July-December 1978 and May-July 1979 at Cedar Bayou (Figure 7). Late summer spawned fish formed less distinct modes readily followed in the periods: 1) December 1977-July 1978 and December 1978-August 1979 off Freeport (Figure 4), 2) February-July 1977 off Port Aransas (Figure 5), 3) December 1977-May 1978 and November 1978-May 1979 in Galveston Bay (Figure 6), and 4) September-December 1978 at Cedar Bayou (Figure 7). Little spawning occurred in June and July,

because few fish 25-60 mm TL were captured from late June through August in the gulf (Figures 4, 5), in Galveston Bay (Figure 6), or at Cedar Bayou (Figure 7).

Discussion

Our findings on *C. arenarius* spawning agree with the limited literature. The small size at maturity agrees with Gunter's (1945) capture of a ripe male only 157 mm TL. The broad March-September spawning period found agrees with many studies, including Franks et al. (1972), Gallaway and Strawn (1974), and Moffett et al. (1979). The fact that spawning occurs in distinct spring and late summer peaks has not been recognized clearly but is supported by: 1) the midsummer lull in spawning that Margraf (1978) noted; 2) the late winter-early spring and early fall spawnings that Juneau (1975) observed; and 3) the distinct modes, one formed in spring and one formed in late summer, in size data of Gunter (1945:76), Christmas and Waller (1973, fig. 8), Gallaway and Strawn (1974, table 24), Swingle and Bland (1974:41), Moffett (1975, fig. 19), and Landry (1977, fig. 23, 24). Multiple spawning peaks also have been reported for other *Cynoscion* spp. such as *C. nothus* (DeVries and Chittenden[6]) and *C. regalis* (Daiber 1957 and Harmic 1958 cited in Thomas 1971; Massmann et al. 1958; Merriner 1976).

SPAWNING AREAS, EARLY NURSERIES, AND MOVEMENTS

Results

Sand seatrout of both spring and late summer groups spawn in the inshore gulf. Spawning and nursery areas of spring spawned groups are indicated by distinct size gradients in length frequencies for May-August 1979 (Figure 9B): 1) an estuarine gradient in which the smallest fish were in the upper estuary at Cedar Bayou while larger ones were in Galveston Bay and at 4.5 m in the gulf, 2) a gradient in the gulf in which the smallest fish were at 7-15 m and sizes increased in deeper water, and 3) another gradient in the gulf in which the smallest fish were at 7-15 m but sizes increased in shallower water. Length frequencies from Cedar Bayou, Galveston Bay, and the gulf off Freeport indicate growth continued in May-August 1979 (Figures 4, 6, 7). Therefore, the first size gradient indicates dispersion of larger juveniles down the estuary. The latter two size gradients indicate outward dispersion of larger young and/or eggs and larvae from spawning grounds near 7-15 m in the gulf to deeper and shallower water. Late summer spawned groups also use inshore gulf spawning grounds as indicated by locations of mature fish at spawning time.

Capture locations of mature and ripe adults at spawning time also suggest an inshore gulf spawning area. Many fish of the late summer 1978 group reached age I and entered the gulf in August 1979 (Figure 4), presumably to spawn near the 7-22 m depths where they were captured; none were captured at 4.5 or 55-100 m (Chittenden unpubl. data), but the 27-46 m depth range was not occupied in that cruise. Five ripe stage fish were captured in April and May 1978 at 14-46 m in the gulf. However, it is not clear how far these fish traveled before spawning.

Discussion

The estuarine size gradient that we found could reflect spawning grounds in the upper estuary, or most probably, spawning grounds that encompass the inshore gulf and/or lower estuary. This gradient probably does not reflect an upper estuarine spawning ground, because the early life history of *C. arenarius* is much like that of the Atlantic croaker, *Micropogonias undulatus*. The Atlantic croaker exhibits egg and/or larval transport to the upper estuary from spawning grounds in the sea (Wallace 1940; Haven 1957) and well-documented estuarine size gradients (Gunter 1945; Haven 1957; Reid and Hoese 1958). Moreover, a similar early life history has been suggested for other Sciaenidae, especially *C. regalis* (many references in Wilk 1979).

Our explanation for the estuarine size gradient conflicts with the size pattern in the gulf. The latter pattern suggests outward dispersal of young and/or transport of eggs and larvae from spawning grounds near 7-15 m. The direction of movement suggested by the estuarine gradient, however, is opposed to the direction of movement suggested by the gulf gradient in which sizes increase inshore. We offer no simple explanation for the apparent dichotomy except that it might reflect: possibly separate estuarine and gulf spawning grounds which might involve temporal

[6]DeVries, D. A., and M. E. Chittenden, Jr. In prep. Spawning, age determination, and population dynamics of the silver seatrout, *Cynoscion nothus*, in the Gulf of Mexico.

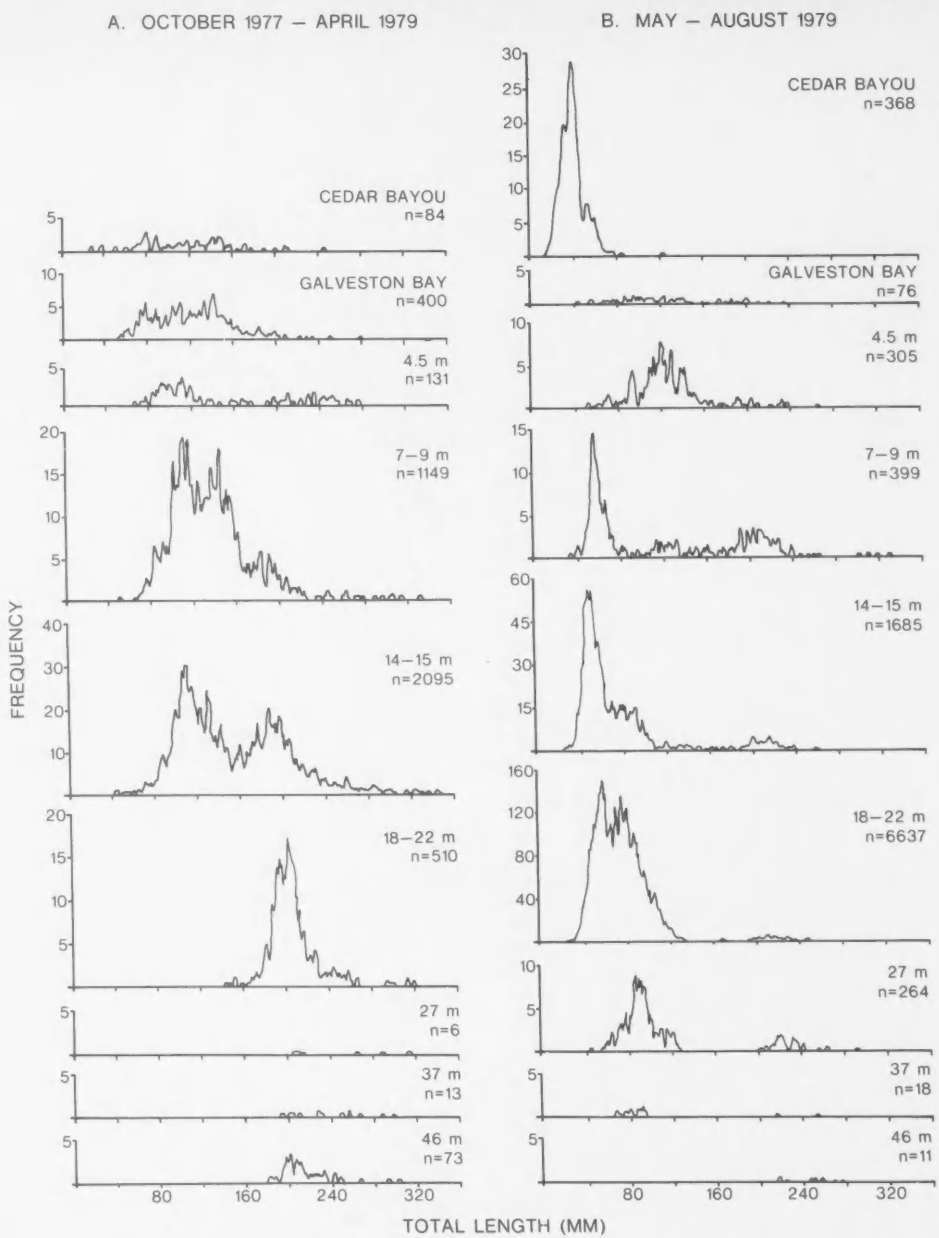

FIGURE 9.—Length frequencies (moving averages of three) of *Cynoscion arenarius* collected at each depth off Freeport and in Galveston Bay and Cedar Bayou, Tex. A. October 1977-April 1979. B. May-August 1979.

differences in spawning, and as noted shortly, the unusual flooding near Galveston Bay during spring 1979 and current transport phenomena which are strongly wind-driven in the gulf and its estuaries. Under nonflood conditions a single gradient of increasing size extended from the upper estuary out to at least 22 m in the gulf (Figure 9A), which suggests that the dichotomous condition in May-August 1979 (Figure 9B) was an exception caused by flooding.

Our data suggest that *C. arenarius* spawns in the shallow inshore gulf, but the extent of its spawning grounds is not yet clear and could vary seasonally. Other workers also have reported evidence of gulf spawning (Gunter 1945; Moffett et al. 1979). Perry (1970) and Franks et al. (1972) captured running ripe *C. arenarius* in the gulf during February and March at 73-91 m (about 105 km offshore) which could indicate spawning offshore in deep water; but the distance these fish traveled before spawning is not clear. Reid (1955), Hoese (1965), and Copeland and Bechtel (1974) reported spawning in estuaries, but they presented little evidence. However, Harmic (1958) found that the closely related *C. regalis* spawned within Delaware Bay.

Clear delineation of the spawning grounds requires understanding how this species passes from spawning grounds to nurseries. The spring and late summer spawning periods of *C. arenarius* coincide with periods of rising sea level in the northern gulf in response to prevailing onshore winds and surface currents (Collier and Hedgpeth 1950; Marmer 1954). Spawning probably is timed to take advantage of this seasonal phenomenon to transport eggs and/or larvae from inshore gulf spawning grounds to estuarine and gulf nurseries as our size composition data indicate. The bayward movement of postlarvae that Simmons and Hoese (1959) reported on incoming tides could be enhanced by rising sea levels and prevailing onshore winds and currents. However, spawning also coincides with seasonal rainfall peaks (Collier and Hedgpeth 1950) which could modify estuarine transport phenomena. Currents and tides in the nearshore northern gulf and its shallow estuaries are influenced greatly by wind and flooding (Collier and Hedgpeth 1950; Smith 1975). Therefore, spawned group strength of *C. arenarius* and its spatial distribution may be influenced greatly by short-term wind and rainfall patterns that affect current transport and, thereby, survival of the eggs and/or larvae as Nelson et al. (1977) reported for Atlantic menhaden, *Brevoortia tyrannus*.

NURSERIES AND LATER MOVEMENTS

Results

Spring and late summer spawned groups use both estuarine and inshore gulf nurseries in their early life, although estuaries may be most important for late summer fish. Recently hatched spring fish were abundant in 1977-79 from May through July in the inshore gulf, in Galveston Bay, and Cedar Bayou (Figures 4-7). Few recently hatched late summer fish were in the inshore gulf in September-November of 1977-78 (Figures 4, 5), but they were common then in Galveston Bay and Cedar Bayou (Figures 6, 7) and were abundant in the gulf in December (Figures 4, 5).

The main nursery of *C. arenarius* in the northwestern gulf lies in water <18 m. Fish >160 mm TL occurred throughout the 4.5-46 m depth range (Figure 9A). However, fish <160 mm TL only occurred in <18 m except in May-August 1979 when recently hatched spring 1979 fish were abundant to 27 m and present to 37 m (Figure 9B). The Gulf nursery probably expands or contracts depending on spawned group strength and factors that determine dispersal of the young. For example, the great abundance of small fish in the gulf during May-August 1979 might be due to increased spawned group strength and/or heavy flooding in the Galveston Bay area in that spring (Barris 1979).

Fish that use estuarine nurseries in their early life enter the gulf during mid and late fall to overwinter. Spring fish grew in the gulf from May through September-October 1977 and 1978 (Figures 4, 5), but thereafter showed no growth or decreased sizes through December. This pattern indicates movement from estuaries to the gulf with the larger fish preceding smaller ones, assuming continued growth in that period. Many recently hatched late summer fish entered the gulf during December 1977 and 1978 (Figures 4, 5), because few were in the gulf before then. Few were in Galveston Bay or Cedar Bayou from December through March (Figures 6, 7), although they were abundant in the gulf.

Late summer spawned groups return to estuaries during midspring after overwintering in the gulf. Although abundant in the gulf in the February-April periods of 1977-79 (Figures 4, 5),

few late summer fish were in the gulf in the following May-July period except in 1977 off Port Aransas. Most must have returned to estuaries in midspring and remained there until they returned to the gulf to spawn in August (Figure 4). Late summer fish were captured in Galveston Bay in May-July (Figure 6), but not in large numbers which may reflect a habitat change by these larger fish or avoidance of the small trawls used there. Sizes of the late summer fish in the gulf remained stable or decreased in July-August 1978 and 1979 (Figure 4). This is similar to the pattern noted in the fall for spring spawned fish and suggests a similar gradual dispersal of the late summer groups to the gulf.

Movements of spring spawned groups as they reach age I are not clear. We captured few age I fish in the spring or following summer except in March and April 1979 in the gulf (Figure 4). Most apparently die after spawning, but our data do not clarify movements of the survivors.

Cynoscion arenarius exhibits little diel variation in size composition. The two spawned groups off Freeport during December 1978 and in April, June, and July 1979 showed little day-night size variation (Figure 4). Some differences—e.g., December 1978—probably reflect growth or movements in the 2-wk period between collections.

Discussion

Our findings on the nurseries and later movements of *C. arenarius* agree with the limited literature, although the complex life history of this species has not been recognized. The fact that the young occur in both estuaries and the inshore gulf has been reported (Gunter 1945; Miller 1965; Christmas and Waller 1973), but these workers did not recognize separate spring and late summer spawned groups nor possible differences in their nurseries. Our finding that *C. arenarius* move in fall from estuaries to overwinter in the gulf has been reported by many workers including Gunter (1938, 1945), Chambers and Sparks (1959), Perret and Caillouet (1974), and Ogren and Brusher (1977) who based their findings only on apparent change in abundance without recognizing size composition changes, or the differences between spring and late summer spawned groups. Movement of "mature" *C. arenarius* in the period April-May from the gulf to estuaries has been reported (Simmons 1950-51 cited in Guest and Gunter 1958; Simmons and Hoese 1959). These might have been late summer fish in agreement with our findings, but these workers did not recognize different spawned groups. Data of Perret and Caillouet (1974, fig. 6), however, show return of late summer fish to Vermillion Bay, La., in April and May. The absence of diel size variation in *C. arenarius* contrasts with its presence in *C. nothus* (DeVries and Chittenden footnote 6).

GROWTH AND AGE DETERMINATION BY LENGTH FREQUENCY

Results

No more than two year classes of *C. arenarius* occurred in any 1 mo in the gulf, in Galveston Bay, or in Cedar Bayou (Figures 4-7). Only one year class was captured from February through April, except possibly in March 1979 off Freeport. Two year classes usually were present in the gulf and in Galveston Bay from May through December—but no more than three spawned groups.

Cynoscion arenarius averages 210-280 mm TL at age I depending on spawned group. Spring fish averaged 160-190 mm TL at 6 mo and 220-280 mm at age I (Figure 10), although many were 200 mm or more at 6 mo and some were 300 mm at age I (Shlossman 1980, tables 1, 2). Late summer fish were slightly smaller, averaging 120-150 mm TL at 6 mo and 210-250 mm at age I (Figure 10), although many were 175 mm or more at 6 mo and some were 300 mm at age I (Shlossman 1980, tables 1, 2). Mean sizes predicted by regression (Figure 10) were 250 mm TL at age I, 425 mm at age II, and 574 mm at age III for late summer fish. Predictions for spring fish were 260 mm TL at age I, 301 mm at age II, and 160 mm at age III. Predictions for spring fish are unrealistic at age III and probably too low at age II, because the simple polynomial regression used describes growth as a parabola.

Growth generally was greatest in warmer months and least in colder months. Both spring and late summer spawned fish grew slowest (5-10 mm TL/30 d) in winter (Figure 11). Spring fish grew fastest (35 mm TL/30 d) from May through October; much variation occurred, however, and zero increments in summer and mid to late fall reflect movement of larger fish from estuaries to the gulf, not lack of growth. Late summer fish grew rapidly in spring; decreased increments in late spring and early summer may reflect movement of larger fish from estuaries to the gulf.

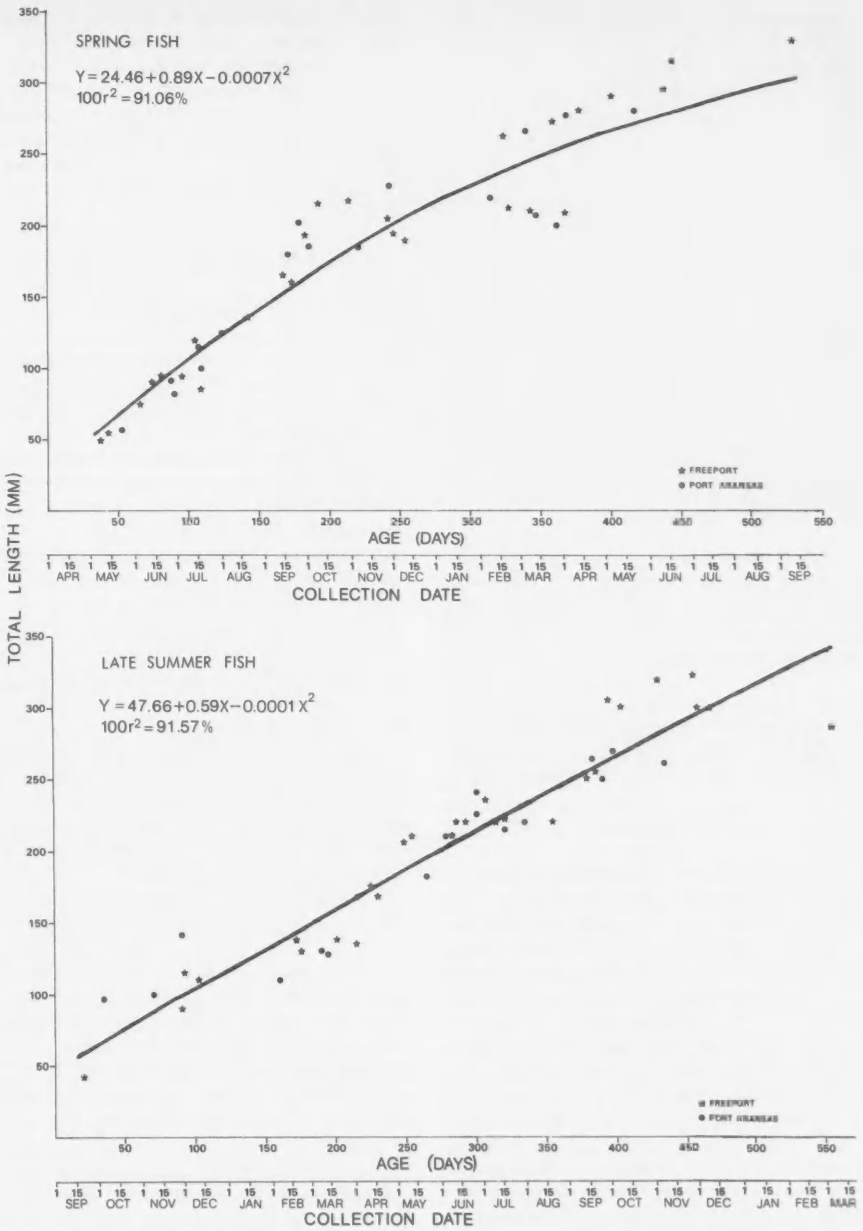
SPRING FISH
Y = 24.46 + 0.89X − 0.0007X²
100r² = 91.06%
FREEPORT
PORT ARANSAS
TOTAL LENGTH (MM)
AGE (DAYS)
COLLECTION DATE
APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP
LATE SUMMER FISH
Y = 47.66 + 0.59X − 0.0001X²
100r² = 91.57%
FREEPORT
PORT ARANSAS
AGE (DAYS)
COLLECTION DATE
SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR

FIGURE 10.—Observed and predicted sizes at age of *Cynoscion arenarius* from the gulf off Freeport and Port Aransas, Tex., for spring spawned fish and late summer spawned fish. Modal sizes (Shlossman 1980, tables 1, 2) were regressed on ages after assigned hatching dates. Regression was significant at $\alpha = 0.01$.

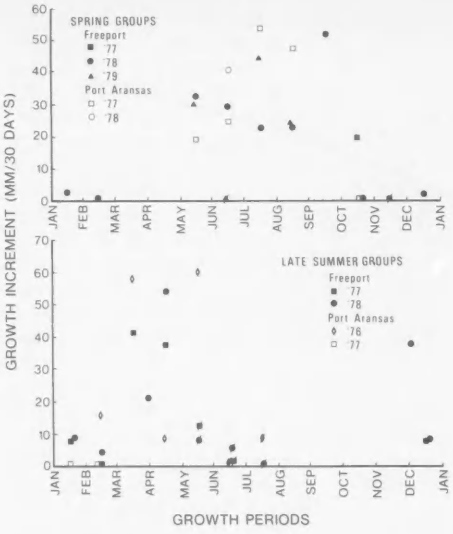

FIGURE 11.—Monthly growth increments of *Cynoscion arenarius* for spring and late summer groups from the Gulf of Mexico. Unadjusted well-defined increment data of Shlossman (1980, tables 1, 2) were converted to growth per 30 d. Increments with a diagonal (/) reflect movement, not necessarily low growth. Negative increments were rounded to zero.

Female *C. arenarius* reach larger sizes than males. All fish >300 mm TL (n = 13) and 88% examined >250 mm (n = 80) were female.

Discussion

Our findings on *C. arenarius* growth agree with the limited literature. Our average growth estimates—210-280 mm TL at age I depending upon the spawned group—agree with data of Perret and Caillouet (1974, fig. 6), but slightly exceed data of Swingle and Bland (1974:41) and estimates of Hoese et al. (1968), McEachron et al. (1977), and Chittenden (1977). Decreased growth in winter agrees with observations of Gunter (1945) and Hoese et al. (1968). Seasonal growth is similar to that of *C. nothus* (DeVries and Chittenden footnote 6), *C. nebulosus* (Pearson 1929; Tabb 1961), and *C. regalis* (Welsh and Breder 1923; Hildebrand and Cable 1934; Merriner 1973). However, *C. arenarius* is larger at age I than its three congeners in the western North Atlantic: 1) *C. nothus*, 130-190 mm SL = 158-229 mm TL (DeVries and Chittenden footnote 6); 2) *C. regalis*, 143-180 mm SL = 173-218 TL (Taylor 1916 in Merriner 1973; Perlmutter et al. 1956; Merriner 1973); and 3) *C. nebulosus*, 116-165 mm SL = 144-201 mm TL (Pearson 1929; Moody 1950; Klima and Tabb 1959; Moffett 1961; Tabb 1961). Our findings that females grow larger than males has been reported (Franks et al. 1972), and similar differences occur in *C. nebulosus* (Pearson 1929; Klima and Tabb 1959; Tabb 1961).

AGE DETERMINATION USING SCALES

General Basis

Cynoscion arenarius can be aged using scales. Annuli were identified using standard criteria (Tesch 1971) and procedures for *C. nebulosus*, *C. nothus*, and *C. regalis* (Klima and Tabb 1959; Tabb 1961; Merriner 1973; DeVries and Chittenden footnote 6). Characters used to identify annuli included: 1) a clear zone between bands of circuli in the anterior field (Figures 12, 13), 2) a band of crowded circuli adjacent to a band of more widely spaced circuli (Figure 12), 3) secondary radii radiating from a clear zone or changed spacing between circuli (Figures 12, 13), 4) cutting over of circuli (Figures 12, 13), and 5) appearance of these characters on all or most scales. Marks identified as false annuli: 1) appeared on only a few scales from a fish, 2) had secondary radii not accompanied by a clear zone or changed spacing of circuli, 3) had a clear zone or changed spacing between circuli not accompanied by other characters, and 4) lacked distinct cutting over. False annuli were common, as Merriner (1973) found for age 0 and age I *C. regalis*.

Results

Few fish had scales with an annulus. Only 159 of 1,602 fish (10%) examined had one annulus and only 6 fish (0.4%) had two annuli. This finding that 10% had one annulus is not consistent with the 99% annual mortality rate reported later. However, the sample aged was biased by arbitrary selection of large fish. Moreover, the annulus primarily forms at 0.5-0.75 yr which is before annual mortality is complete.

The first annulus forms from April through November, although spring and late summer spawned fish may form annuli at different times. Marginal increments in late summer fish were smallest in spring and early summer (Figure 14),

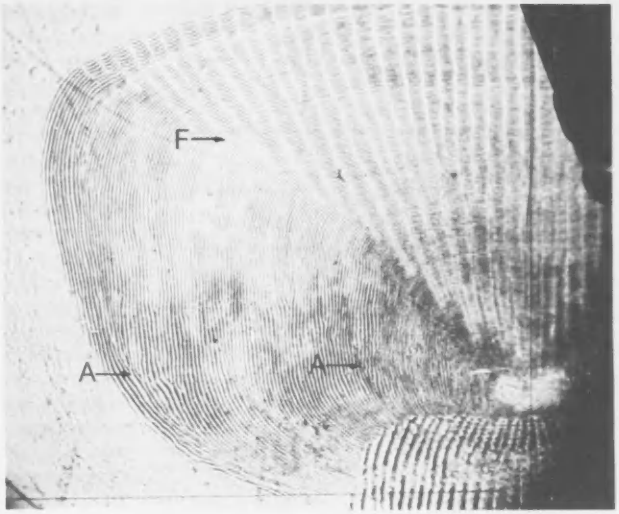

FIGURE 12.—Scale from a spring spawned 338 mm TL *Cynoscion arenarius* captured in September showing two annuli (A). The first annulus shows cutting over in the lateral field and changed spacing of circuli associated with secondary radii in the anterior field. The second annulus shows cutting over in the lateral field and a clear zone between circuli in the anterior field. A false annulus (F) had a few secondary radii but lacked changed spacing between circuli or a clear zone and distinct cutting over and was absent on most scales.

FIGURE 13.—Scale from a late summer spawned 300 mm TL *Cynoscion arenarius* captured in December showing one annulus (A). Note the cutting over in the lateral field and secondary radii in conjunction with a clear zone between circuli in the anterior field.

so that their first annulus primarily formed from April through July. Marginal increments in spring fish were smallest in late summer and fall, so that their first annulus formed primarily from September (possibly August) through November. Therefore, both spring and late summer fish primarily formed their first annulus at about 0.5-0.75 yr of age.

Fish with one annulus were 136-329 mm TL. The percentage having a first annulus increased with size: 1) 8% at 150-199 mm TL (n = 518), 2) 24% at 200-249 mm (n = 268), 3) 52% at 250-299 mm (n = 77), and 4) 71% at 300 mm and greater (n = 14). Fish with two annuli were 265-338 mm TL.

Back-calculated lengths were smaller than lengths at age determined from length frequencies. Lengths at annulus formation for spring fish using Jones' (1958, equation 2) formula were 81-257 mm TL, and the mean was 162 mm with 95% confidence limits of 154-171 mm. Back-calculated lengths at annulus formation for late summer fish were 96-255 mm TL, and the mean was 178 mm with 95% confidence limits of 169-186 mm. These data support analyses of marginal increments that indicate the first annulus primarily forms at 0.5-0.75 yr, because lengths at age I determined from length frequencies were 220-280 mm TL for spring fish and 210-250 mm for late summer fish. The back-calculated size range of 81-257 mm TL for spring fish agrees with their sizes at age 0 during summer and early fall (Figures 4, 5). Similarly, the back-calculated size range of 96-255 mm TL for late summer fish agrees

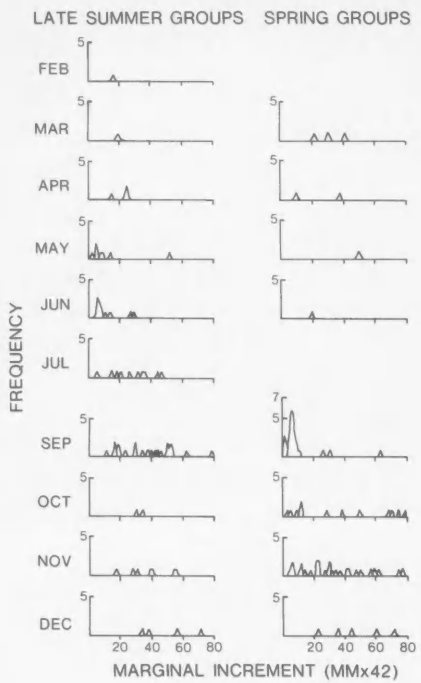

FIGURE 14.—Monthly marginal increments for *Cynoscion arenarius* with one mark.

with their sizes at age 0 in spring and early summer (Figures 4, 5).

Repeated examination suggests that age determination was consistent. We found 86% agreement in a second reading of scales from 361 fish 120-338 mm TL, including all fish initially determined to have an annulus. Disagreement occurred primarily when the scales had a mark close to the margin or had one annulus and one false annulus.

Discussion

Scales can be used to age *C. arenarius*, but length-frequency analysis is simpler and at least as accurate except possibly with fish much older than those we caught. Separate spring and late summer spawning periods complicate age determination. Age, growth, and mortality estimates should be based on individual spawned groups to avoid misinterpretation. Valid estimates require assignment of individuals to correct spawned groups; and that requires length-frequency analysis, because annulus formation occurs over a broad time period in both spring and late summer groups. Exact age determination may be impossible for the apparently few fish older than say, age II or III. Their ages probably would not be distinct in length frequencies and a spawned group probably could not be assigned.

Causes of annulus formation in *C. arenarius* are not clear, although temporary growth cessation may be associated with movements between estuaries and the gulf and/or gonad development. Annulus formation in late summer fish coincides with their spring movement to estuaries and gonad development. Similarly, annulus formation in spring fish coincides with fall movements from estuaries. However, many spring fish use only gulf nurseries in their early life which might minimize mark formation in those fish. False annulus formation might be associated with movements between estuaries and the gulf. *Cynoscion arenarius* and *C. regalis* are similar in that both migrate between the sea and estuaries (Welsh and Breder 1923; present studies) and their scales exhibit many false annuli (Merriner 1973; present studies). In contrast, *C. nothus*, a gulf resident, exhibits few false annuli (DeVries and Chittenden footnote 6).

MAXIMUM SIZE, LIFESPAN, AND MORTALITY

Cynoscion arenarius is small and short lived. The largest of the 13,780 fish we captured was 342 mm TL, although few exceeded 300 mm. Our findings agree with Gunter (1945), Hildebrand (1954), Perry (1970), and Chittenden and McEachran (1976) who captured fish to 377 mm TL but few >300 mm. Many other studies have reported even smaller maxima including Miller (1965), Christmas and Waller (1973), and Perret and Caillouet (1974). The only published records much >300-375 mm TL include a few trawl-caught fish 425-497 mm TL from the north-central gulf (Franks et al. 1972; Adkins and Bowman 1976) and off Texas (Mohsin 1973), 590 and 540 mm TL gill net caught fish from northwestern Florida (Vick 1964; Trent and Pristas 1977), and fish as large as 483 and 503 mm TL captured in Galveston Bay, Tex., by commercial and recreational fishermen, respectively (Heffernan et al.[7]). The latter study gave size data

[7]Heffernan, T. L., A. W. Green, L. W. McEachron, M. G. Weixelman, P. C. Hammerschmidt, and R. A. Harrington. 1976. Survey of finfish harvest in selected Texas

from fisheries whose gear was biased seriously to capture large fish about 12 mo and older. However, even these fish averaged only 280 mm TL in recreational catches and 343 mm in commercial catches; and few were >330 mm and 406 mm TL, respectively.

The maximum lifespan of *C. arenarius* typically is 1-2 yr at most for trawl-caught fish and possibly as much as 2-3 yr for other gear. In the period October 1977-April 1979, 90% of the 3,988 fish that we captured off Freeport were <215 mm TL (Figure 15), 99% were <280 mm, and 99.5% were <300 mm. Similarly, of the 2,073 fish collected off Port Aransas during February 1977-July 1978 (Figure 15), 90% were <210 mm TL, 99% were <260 mm, and 99.5% were <275 mm. A t_L value of 1-2 yr at most is reasonable for the Beverton-Holt model parameter (Gulland 1969) for trawl-caught *C. arenarius* because fish >260-300 mm TL made up <0.5-1.0% of our catch. This is about the average size at age I (210-280 mm TL), which many individuals exceed, and approaches the maximum sizes usually reported. Our trawling, moreover, shows the scarcity of fish with more than one annulus, a disappearance of all fish by 14-18½ mo of age (Table 3), and agrees with Chittenden and McEachran's (1976) suggestion that the typical lifespan is no more than 1-2 yr. Even recreational and commercial gear seriously selective for larger sizes (references cited above) catch fish whose typical maximum age appears to be only 2-3 yr, at most, because mean sizes at these ages predicted by polynomial regression were 431 mm TL at age II and 574 mm at age III for late summer fish and a probably unrealistically low 301 mm at age II for spring fish.

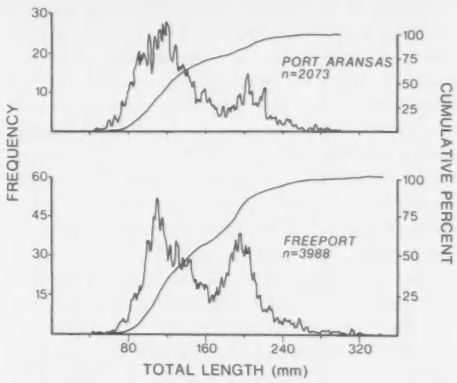

FIGURE 15.—Length frequency (moving average of three) and cumulative percentage of all *Cynoscion arenarius* collected in the Gulf of Mexico off Freeport, Tex., October 1977-April 1979 and off Port Aransas, Tex., February 1977-July 1978.

Sand seatrout has a total annual mortality rate that approaches 100% and has a best estimate of 99.79% based on trawling data. Time-specific values of total annual mortality ($1 - S$) were calculated for each individual month from the expression $S = N_t/N_o$ where S = rate of survival and N_o and N_t are the number of fish collected from consecutive spring or late summer groups. Of the 20 mo when collections were made off Freeport, only one spring group was present in 14 mo and only one late summer group was present in 17 mo (Figure 4). Of the 14 mo when collections were made off Port Aransas, only one spring group was present in 13 mo and only one late summer group was

bays. Tex. Parks Wildl. Dep., Coastal Fish Branch, Proj. Rep. 2-231-R-1, 116 p.

TABLE 3.—Periods of time, sizes, and ages when spawned groups of *Cynoscion arenarius* were last captured off Freeport and Port Aransas, Tex.

Spawned group and location	Disappeared in the period	TL (mm)	Age (mo)	Comments
Spring 1976:				
Port Aransas	5 Apr.-28 May 1977	260-295	12-14	Few specimens ever captured
Late summer 1976:				
Freeport	4 Nov.-3 Dec. 1977	275-340	14-15	Few specimens ever captured
Port Aransas	10 Nov. 1977	240-285	14-15	
Spring 1976:				
Freeport	14 June-15 Sept. 1978	295-340	14½-17½	Few captured after December 1977
Port Aransas	8 Mar. 1978	250-280	11-12	Few captured after November 1977
Late summer 1977:				
Freeport	13 Dec. 1978-12 Mar. 1979	280-320	15½-18½	Few captured after September 1978
Port Aransas	28 June 1978	240	11	
Spring 1978:				
Freeport	21 June 1978	305-325	14½	Few captured after April 1979
Port Aransas	15 July 1978	80-150	4½	Still being recruited when last collection was made
Last summer 1978:				
Freeport	22 Sept. 1979	205-305	13	Still abundant when last collection was made; sizes not distinct

present in 11 mo (Figure 5). The apparent values of $1 - S$ were 100% within each month when N_t was zero. In six other months the youngest group in the ratio N_t/N_o was incompletely recruited off Freeport, so that the following mortality rates would be underestimates: 1) June 1978, 99.2%, spring fish; September 1978, 98.9%, spring fish; 2) May 1979, 99.5%, spring fish; June 1979, 99.9%, spring fish; August 1979, 99.0%, spring fish; and 3) December 1978, 98.8%, late summer fish. Because the youngest spawned group in the ratio strongly showed incomplete recruitment, realistic mortality estimates were not possible for the following months: 1) spring groups, May 1977, Port Aransas; 2) late summer groups, September, October, and November 1977, Port Aransas; 3) spring groups, May 1978, Freeport; and 4) late summer groups, December 1977, September 1979, Freeport. Following the first procedure of Robson and Chapman (1961), we calculated an average value of $1 - S$ = 99.79% by pooling identifiable N_o and N_t values from each month except the seven in which the youngest spawned group strongly showed incomplete recruitment.

Our observed estimates agree with the theory (Royce 1972:238) that the total annual mortality rate is about 90% if the lifespan is about 2 yr and approaches 100% if 1 yr. Our high mortality estimates are consistent with maximum sizes and length frequencies in many published faunal studies based on trawling in estuarine and gulf waters. Theoretical values that $1 - S$ = 80-90% based on lifespans of 2-3 yr appear to be lowest tenable values even if the data include recreational or trammel/gill net caught fish.

TOTAL WEIGHT-, GIRTH-, AND STANDARD LENGTH-TOTAL LENGTH RELATIONS

Total weight-total length, girth-total length, and standard length-total length relationships are presented in Table 4. Regressions of total weight on total length were significantly different in elevation between sexes (F = 5.38; 1, 1,501 df; α = 0.05) but not in slope (F = 2.41; 1, 1,500 df; α = 0.05). Calculated slopes significantly exceeded β = 3.0 at α = 0.5 (data pooled, t = 18.85; males, t = 15.10; females, t = 14.85).

GENERAL DISCUSSION

The fact that *C. arenarius* produces two distinct, major spawned groups each year may be important to its systematic status, management, and to understanding its population fluctuations.

The temporal separation of the spawned groups implies reproductive isolation, the extent of which remains to be determined. The existence of the two spawned groups—and their systematic status—must be considered in resolving the status of *C. arenarius*. Ginsburg (1929), Mohsin (1973), and Weinstein and Yerger (1976) did not indicate the spawned groups studied. The two spawned groups may be separate populations or, possibly, separate species. That should be determined and considered in management because fishing could affect them differently.

The production of two major spawned groups each year would minimize year to year population fluctuations even though *C. arenarius* is short lived and little more than an annual crop. As DeVries and Chittenden (footnote 6) noted for *C. nothus*, each spawned group buffers population stability as a multiple year class structure buffers longer lived species. Ricker reproduction curves (Ricker 1954, 1975) might be useful to simulate fluctuations of multiple spawned-group stocks.

Many aspects of the life history and population dynamics of *C. arenarius* differ from *C. regalis* in the Middle Atlantic Bight north of Cape Hatteras, but *C. arenarius* appears similar to *C. regalis* south of Cape Hatteras. In general, it appears that for *C. arenarius*: 1) spawning lasts from March through September but mainly occurs in two peaks, a spring period (March-May) and a late summer period (August-September); 2) maturity is reached at 140-180 mm TL as they approach age I and spawn; 3) maximum size typically is 350-375 mm TL, but most fish are much smaller so that *C. arenarius* is not a major commercial food fish; 4) maximum age typically is 1-2 yr, or 3 yr at most; 5) total annual mortality rate is 80-90% or more, our best estimate being 99%, and 6) fish reach 210-280 mm TL at age I.

The life history of *C. regalis* in the Middle Atlantic Bight is more difficult to enumerate, because it makes north-south and onshore-offshore migrations (Pearson 1932; Nesbit 1954; Wilk 1979). Moreover, at least two intermixing populations may occur there (Nesbit 1954; Perlmutter et al. 1956; Seguin 1960), although stocks remain undefined (Joseph 1972; Merriner 1973; Wilk 1979). However, it appears that *C. regalis* north of Cape Hatteras 1) spawn from May to August with one peak period about April-June (statements of sev-

TABLE 4.—Total weight-total length, total length-girth, and standard length-total length regressions for *C. arenarius* with supporting statistics. All regressions were significant at $\alpha = 0.05$. Measurements are grams and millimeters.

Equation	n	TL range	$100r^2$	Residual MS	Corrected total SSx	Corrected total SSy	$\bar{X}$	$\bar{Y}$
$\log_{10} TW = -5.6609 + 3.2572 \log_{10} TL$ (males)	851	—	97.7	0.0027	9.52	103.35	2.2096	1.5359
$\log_{10} TW = -5.6325 + 3.2420 \log_{10} TL$ (females)	653	—	98.4	0.0025	9.48	101.32	2.2346	1.1612
$\log_{10} TW = -5.4698 + 3.1715 \log_{10} TL$ (males, females, immatures)	1,776	40-338	98.5	0.0032	38.67	394.07	2.1780	1.4379
$G = 1.197 + 0.512\ TL$	1,776	40-338	97.0	20.20	1,220,591 (G)		159.2	82.7
$TL = 2.269 + 1.897\ G$	1,776	40-338	97.0	74.80	4,519,719 (TL)		82.7	159.2
$SL = -6.49 + 0.85\ TL$	1,776	40-338	99.7	4.56	3,369,130 (SL)		159.2	128.8
$TL = 8.01 + 1.17\ SL$	1,776	40-338	99.7	6.30	4,641,233 (TL)		128.8	159.2

eral workers including Welsh and Breder 1923; Hildebrand and Schroeder 1928; Nesbit 1954) or with two peak periods about June and July (Daiber 1957 and Harmic 1958 cited in Thomas 1971); 2) mature at 160-230 mm TL (130-190 mm SL) and spawn at age I throughout their range (Merriner 1976), the validity of which might be reexamined for the New York Bight, because females in Delaware Bay first spawn at age III-IV when fish average 280-330 mm TL (Welsh and Breder 1923); 3) more or less commonly reached maximum weights of 4.54-7.72 kg (10-17 lb) or more (Welsh and Breder 1923; Wilk 1979), maximum lengths of about 400-600 mm TL or more (Welsh and Breder 1923; Hildebrand and Schroeder 1928; Nesbit 1954; Perlmutter et al. 1956), and average long enough to support important commercial food fisheries (Nesbit 1954; Perlmutter et al. 1956; Joseph 1972; Merriner 1973); 4) commonly reach or once reached ages of 3-7 yr (Welsh and Breder 1923; Nesbit 1954; Perlmutter et al. 1956; Massmann 1963; Wilk 1979), although Massmann (1963) described a long-term reduction in size and presumably age composition in Chesapeake Bay; 5) have total annual mortality rates of 48-73% (Nesbit 1954; Massmann 1963; Merriner 1973) which agree with theoretical estimates of 48-68% for lifespans of 4-7 yr assuming negative exponential survivorship; and 6) reach 170-220 mm TL (143-180 mm SL) at age I (Thomas 1971, table 13; Merriner 1973, table 2.23), although reported growth varies and ages may be questionable (Merriner 1973; Wilk 1979).

Although less has been published from south of Cape Hatteras, it appears that those *C. regalis* generally 1) spawn from March through August with a peak about March-June (Hildebrand and Cable 1934; Mahood 1974; Merriner 1976), although a second smaller peak may occur in July-August (Merriner 1976); 2) mature at 160-230 mm TL and spawn at age I throughout their range (Merriner 1976); 3) are much smaller than more northern fish, because few have been reported much >350-375 mm TL (unpubl. data of Anderson from 1930 to 1932 in Mahood 1974, fig. 11; Wolff 1972; Hoese 1973; Mahood 1974; Wenner[8]); 4) commonly reach ages of only 2-3 yr (Wolff 1972; Merriner 1973: data from Morehead City, N.C., fig. 2.7) although age IV fish were common in Pamlico Sound at Hatteras, N.C. (Merriner 1973, fig. 2.7); 5) have total annual mortality rates of 48-73% (Merriner 1973), which might be too low if maximum age typically is 2-3 yr; and 6) average 180-195 mm TL (150-160 mm SL) at age I (Merriner 1973, table 2.11).

The preceding comparisons indicate typical maximum sizes and ages of *C. regalis* differ north and south of Cape Hatteras, and this suggests different total annual mortality rates. New York Bight fish might be older at maturity than fish south of Cape Hatteras, although Merriner (1976) felt they matured at age I throughout their range. Although *C. regalis* migrates north-south and stocks need study, tagging (Nesbit 1954) indicated that North Carolina does not contribute much to New York Bight catches at least. Therefore, movements should not affect the basic conclusion of zoogeographic change in population dynamics at Cape Hatteras. Large *C. regalis* do appear near Cape Hatteras at times as Pearson (1932) and Merriner (1973, fig. 2.7, data from Hatteras) observed, but these may be from northern stocks that had moved south (Pearson 1932).

Zoogeographic changes in the life history and population dynamics of *C. regalis* support the suggestion (White and Chittenden 1977) that species widely distributed along the east coast of the United States may show marked change in life

[8]E. Wenner, Assistant Marine Scientist, South Carolina Department of Wildlife and Marine Resources, P.O. Box 12559, Charleston, SC 29400, pers. commun. August 1980.

history and population dynamics at Cape Hatteras. This phenomenon needs to be considered in management; because given rates of fishing, for example, would more strongly affect stocks north of Cape Hatteras.

In contrast to the zoogeographic differences within *C. regalis*, the life history and population dynamics of *C. arenarius* appear similar to *C. regalis* south of Cape Hatteras. Reproduction is similar in age at maturation, age at first spawning, and the spawning period. The bimodal spawning periodicity in *C. arenarius* differs, at first glance, from that of *C. regalis* south of Cape Hatteras, but this has been recognized only recently for *C. arenarius* and may exist in southern *C. regalis* (Merriner 1976). Differences in typical maximum sizes and ages are small, if real, and this suggests mortality rates more similar than present data indicate. The similarity of the life history and population dynamics of *C. arenarius* to that of *C. regalis* south of Cape Hatteras is consistent with Weinstein and Yerger's (1976) suggestion that they may be one species.

Finally, the population dynamics of *C. arenarius*, including its short lifespan, high mortality rate, and rapid turnover of biomass, are similar to those of *C. nothus* (DeVries and Chittenden footnote 6) and Atlantic croaker of the Carolinean Province (White and Chittenden 1977; Chittenden 1977). This supports the suggestion (Chittenden and McEachran 1976; Chittenden 1977) that the abundant species of the white and brown shrimp communities in the gulf have evolved towards a common pattern of population dynamics. Moreover, Chittenden's (1977) simulations on Atlantic croaker could serve as a first approximation of the effects of harvesting *C. arenarius*, and *C. regalis*, south of Cape Hatteras.

ACKNOWLEDGMENTS

We are much indebted to D. DeVries, P. Geoghegan, M. Murphy, M. Burton, T. Crawford, J. Pavela, M. Rockett, J. Ross, B. Slingerland, G. Standard, H. Yette, and Captains H. Forrester, J. Forrester, M. Forrester, P. Smirch, and A. Smircic for assistance in field collections. We also thank the Texas Parks and Wildlife Department, and particularly the crews of the *Drum II* (L. Benefield, L. Gale, and C. Wilkes) and *Western Gulf* (T. Cody, K. Rice, Captain D. Perez, and D. Mejorado) for their cooperation and assistance. B. Pridgeon of Texas A&M University provided data from Cedar Bayou, and E. Wenner of the South Carolina Department of Wildlife and Marine Resources provided data on length frequency of *C. regalis* in trawl catches from South Carolina estuarine surveys for 1973-78 inclusive. T. Bright, R. Noble, J. Ross, and K. Strawn reviewed the manuscript. Financial support was provided, in part, by the Texas Agricultural Experiment Station; by the Strategic Petroleum Reserve Program, Department of Energy; and by the Texas A&M University Sea Grant College Program, supported by the NOAA Office of Sea Grant, Department of Commerce.

LITERATURE CITED

ADKINS, G., AND P. BOWMAN.
1976. A study of the fauna in dredged canals of coastal Louisiana. La. Wildl. Fish. Comm., Tech. Bull. 18, 72 p.

BAGENAL, T. B., AND E. BRAUM.
1971. Eggs and early life history. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, 2d ed., p. 166-198. Blackwell Sci. Publ., Oxf.

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, AND W. B. SCOTT.
1970. A list of common and scientific names of fishes from the United States and Canada. 3d ed. Am. Fish. Soc., Spec. Publ. 6, 149 p.

BARRIS, R.
1979. Some bayous reach 100-year level. Houston Post, April 21, 25A.

CHAMBERS, G. V., AND A. K. SPARKS.
1959. An ecological survey of the Houston ship channel and adjacent bays. Publ. Inst. Mar. Sci., Univ. Tex. 6:213-250.

CHITTENDEN, M. E., JR.
1977. Simulations of the effects of fishing on the Atlantic croaker, *Micropogon undulatus*. Gulf Caribb. Fish. Inst. Proc. 29th Annu. Sess., p. 68-86.

CHITTENDEN, M. E., JR., AND J. D. MCEACHRAN.
1976. Composition, ecology, and dynamics of demersal fish communities on the northwestern Gulf of Mexico continental shelf, with a similar synopsis for the entire Gulf. Sea Grant Publ. TAMU-SG-76-208, 104 p.

CHRISTMAS, J. Y., AND R. S. WALLER.
1973. Estuarine vertebrates, Mississippi. *In* J. Y. Christmas (editor), Cooperative Gulf of Mexico estuarine inventory and study, Mississippi, p. 320-434. Gulf Coast. Res. Lab.

COLLIER, A., AND J. W. HEDGPETH.
1950. An introduction to the hydrography of tidal waters of Texas. Publ. Inst. Mar. Sci., Univ. Tex. 1(2):121-194.

COPELAND, B. J., AND T. J. BECHTEL.
1974. Some environmental limits of six Gulf coast estuarine organisms. Contrib. Mar. Sci. 18:169-204.

DAIBER, F. C.
1957. The sea trout. Estuarine Bull. 2(5), 6 p.

DARNELL, R. M.
1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publ. Inst. Mar. Sci., Univ. Tex. 5:353-416.

DEVRIES, D. A.
1979. Aspects of the life history of the silver seatrout, *Cynoscion nothus*, in the Gulf of Mexico. M. S. Thesis, Texas A&M Univ., College Station, 59 p.
DIENER, R. A., A. INGLIS, AND G. B. ADAMS.
1974. Stomach contents of fishes from Clear Lake and tributary waters, a Texas estuarine area. Contrib. Mar. Sci. 18:7-17.
FRANKS, J. S., J. Y. CHRISTMAS, W. L. SILER, R. COMBS, R. WALLER, AND C. BURNS.
1972. A study of nektonic and benthic faunas of the shallow Gulf of Mexico off the state of Mississippi as related to some physical, chemical and geological factors. Gulf Res. Rep. 4:1-148.
GALLAWAY, B. J., AND K. STRAWN.
1974. Seasonal abundance and distribution of marine fishes at a hot-water discharge in Galveston Bay, Texas. Contrib. Mar. Sci. 18:71-137.
GINSBURG, I.
1929. Review of the weakfishes (*Cynoscion*) of the Atlantic and Gulf coasts of the United States, with a description of a new species. Bull. U.S. Bur. Fish. 45:71-85.
GUEST, W. C., AND G. GUNTER.
1958. The sea trout or weakfishes (Genus *Cynoscion*) of the Gulf of Mexico. Gulf States Mar. Fish. Comm., Tech. Summ. 1, 40 p.
GULLAND, J. A.
1969. Manual of methods for fish stock assessment. Part I. Fish population analysis. FAO Man. Fish. Sci. 4, 154 p.
GUNTER, G.
1938. Seasonal variations in abundance of certain estuarine and marine fishes in Louisiana, with particular reference to life histories. Ecol. Monogr. 8:313-346.
1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci., Univ. Tex. 1:1-190.
GUTHERZ, E. J., G. M. RUSSELL, A. F. SERRA, AND B. A. ROHR.
1975. Synopsis of the northern Gulf of Mexico industrial and foodfish industries. Mar. Fish. Rev. 37(7):1-11.
HARMIC, J. L.
1958. Some aspects of the development and the ecology of the pelagic phase of the gray squeteague, *Cynoscion regalis* (Bloch and Schneider) in the Delaware estuary. Ph.D. Thesis, Univ. Delaware, 168 p.
HAVEN, D. S.
1957. Distribution, growth, and availability of juvenile croaker, *Micropogon undulatus*, in Virginia. Ecology 38:88-97.
HILDEBRAND, H. H.
1954. A study of the fauna of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. Publ. Inst. Mar. Sci., Univ. Tex. 3:229-366.
1955. A study of the fauna of the pink shrimp (*Penaeus duorarum* Burkenroad) grounds in the Gulf of Campeche. Publ. Inst. Mar. Sci., Univ. Tex. 4(1):169-232.
HILDEBRAND, S. F., AND L. E. CABLE.
1934. Reproduction and development of whitings or kingfishes, drums, spot, croaker, and weakfishes or seatrouts, family Sciaenidae, of the Atlantic coast of the United States. Bull. U.S. Bur. Fish. 48:41-117.
HILDEBRAND, S. F., AND W. C. SCHROEDER.
1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43(1), 366 p.
HOESE, H. D.
1965. Spawning of marine fishes in the Port Aransas, Texas area as determined by the distribution of young and larvae. Ph.D. Thesis, Univ. Texas, Austin, 144 p.
1973. A trawl study of nearshore fishes and invertebrates of the Georgia coast. Contrib. Mar. Sci. 17:63-98.
HOESE, H. D., B. J. COPELAND, F. N. MOSELY, AND E. D. LANE.
1968. Fauna of the Aransas Pass Inlet, Texas. III. Diel and seasonal variations in trawlable organisms of the adjacent area. Tex. J. Sci. 20:33-60.
JONES, R.
1958. Lee's phenomenon of "apparent change in growth-rate" with particular reference to haddock and plaice. Int. Comm. Northwest Atl. Fish., Spec. Publ. 1:229-242.
JOSEPH, E. B.
1972. The status of the sciaenid stocks of the middle Atlantic coast. Chesapeake Sci. 13:87-100.
JUNEAU, C. L., JR.
1975. An inventory and study of the Vermilion Bay-Atchafalaya Bay complex. La. Wildl. Fish. Comm., Tech. Bull. 13, 153 p.
KLIMA, E. F., AND D. C. TABB.
1959. A contribution to the biology of the spotted weakfish, *Cynoscion nebulosus*, (Cuvier) from northwest Florida, with a description of the fishery. Fla. Board Conserv., Mar. Res. Lab. Tech. Ser. 30, 25 p.
LANDRY, A. M., JR.
1977. Life history and susceptibility of fishes in Galveston Bay, Texas to power-plant cooling-water operations. Ph.D. Thesis, Texas A&M Univ., College Station, 367 p.
MAHOOD, R. K.
1974. Seatrout of the genus *Cynoscion* in coastal waters of Georgia. Ga. Dep. Nat. Resour., Contrib. Ser. 26, 36 p.
MARGRAF, F. J.
1978. The abundance and distribution of fishes in the cooling-water canal system of an electric generating station: with emphasis on the effect of cooling towers. Ph.D. Thesis, Texas A&M Univ., College Station, 106 p.
MARMER, H. A.
1954. Tides and sea level in the Gulf of Mexico. *In* P. S. Galtsoff (coordinator), Gulf of Mexico, its origin, waters, and marine life, p. 101-118. U.S. Fish Wildl. Serv., Fish. Bull. 55.
MASSMANN, W. H.
1963. Annulus formation on the scales of weakfish, *Cynoscion regalis*, of Chesapeake Bay. Chesapeake Sci. 4:54-56.
MASSMANN, W. H., J. P. WHITCOMB, AND A. L. PACHECO.
1958. Distribution and abundance of gray weakfish in the York River system, Virginia. Trans. N. Am. Wildl. Conf. 23:361-369.
MCEACHRON, L. W., C. R. SHAW, AND A. W. MOFFETT.
1977. A fishery survey of Christmas, Drum, and Bastrop Bays, Brazoria County, Texas. Tex. Parks Wildl. Dep., Tech. Ser. 20, 83 p.
MERRINER, J. V.
1973. Assessment of the weakfish resource, a suggested management plan, and aspects of life history in North Carolina. Ph.D. Thesis, North Carolina State Univ., Raleigh, 201 p.
1976. Aspects of the reproductive biology of the weakfish, *Cynoscion regalis* (Sciaenidae), in North Carolina. Fish. Bull., U.S. 74:18-26.
MILLER, J. M.
1965. A trawl survey of the shallow Gulf fishes near Port Aransas, Texas. Publ. Inst. Mar. Sci., Univ. Tex. 10:80-107.

MOFFETT, A. W.
1961. Movements and growth of spotted seatrout, *Cynoscion nebulosus* (Cuvier) in west Florida. Fla. State Board Conserv., Tech. Ser. 36, 35 p.
1975. The hydrography and macro-biota of the Chocolate Bayou estuary, Brazoria County, Texas (1969-1971). Tex. Parks Wildl. Dep., Tech. Ser. 14, 72 p.
MOFFETT, A. W., L. W. MCEACHRON, AND J. G. KEY.
1979. Observations on the biology of sand seatrout (*Cynoscion arenarius*) in Galveston and Trinity Bays, Texas. Contrib. Mar. Sci. 22:163-172.
MOHSIN, A. K. MOHAMMAD.
1973. Comparative osteology of the weakfishes (*Cynoscion*) of the Atlantic and Gulf coasts of the United States (Pisces - Sciaenidae). Ph.D. Thesis, Texas A&M Univ., College Station, 148 p.
MOODY, W. D.
1950. A study of the natural history of the spotted trout, *Cynoscion nebulosus*, in the Cedar Key, Florida, area. Q. J. Fla. Acad. Sci. 12:147-171.
NELSON, W. R., M. C. INGHAM, AND W. E. SCHAAF.
1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull., U.S. 75:23-41.
NESBIT, R. A.
1954. Weakfish migration in relation to its conservation. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 115, 81 p.
OGREN, L. H., AND H. A. BRUSHER.
1977. The distribution and abundance of fishes caught with a trawl in the St. Andrew Bay system, Florida. Northeast Gulf Sci. 1:83-105.
PEARSON, J. C.
1929. Natural history and conservation of redfish and other commercial sciaenids on the Texas coast. Bull. U.S. Bur. Fish. 44:129-214.
1932. Winter trawl fishery off the Virginia and North Carolina coasts. U.S. Bur. Fish. Invest. Rep. 10, 31 p.
PERLMUTTER, A. W., W. S. MILLER, AND J. C. POOLE.
1956. The weakfish (*Cynoscion regalis*) in New York waters. N.Y. Fish Game J. 3:1-43.
PERRET, W. S., AND C. W. CAILLOUET, JR.
1974. Abundance and size of fishes taken by trawling in Vermilion Bay, Louisiana. Bull. Mar. Sci. 24:52-75.
PERRY, J. A.
1970. A study of the bottom fish population in the offshore waters of Mississippi by trawl survey. M.S. Thesis, Univ. Mississippi, 112 p.
REID, G. K., JR.
1955. A summer study of the biology and ecology of East Bay, Texas. Part I. Introduction, description of area, methods, some aspects of the fish community, the invertebrate fauna. Tex. J. Sci. 7:316-343.
REID, G. K., AND H. D. HOESE.
1958. Size distribution of fishes in a Texas estuary. Copeia 1958:225-231.
RICKER, W. E.
1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559-623.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.
ROBSON, D. S., AND D. G. CHAPMAN.
1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90:181-189.
ROESSLER, M. A.
1970. Checklist of fishes in Buttonwood Canal, Everglades National Park, Florida, and observations on the seasonal occurrence and life histories of selected species. Bull. Mar. Sci. 20:860-893.
ROITHMAYR, C. M.
1965. Industrial bottomfish fishery of the northern Gulf of Mexico, 1959-63. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 518, 23 p.
ROYCE, W. F.
1972. Introduction to the fishery sciences. Acad. Press, N.Y., 351 p.
SEGUIN, R. T.
1960. Variation in the middle Atlantic coast population of the gray squeteague, *Cynoscion regalis* (Bloch and Schneider) 1801. Ph.D. Thesis, Univ. Delaware, Newark, 84 p.
SHLOSSMAN, P. A.
1980. Aspects of the life history of the sand seatrout, *Cynoscion arenarius*, in the Gulf of Mexico. M.S. Thesis, Texas A&M Univ., College Station, 75 p.
SIMMONS, E. G., AND H. D. HOESE.
1959. Studies on the hydrography and fish migrations of Cedar Bayou, a natural tidal inlet on the central Texas coast. Publ. Inst. Mar. Sci., Univ. Tex. 6:56-80.
SMITH, N. P.
1975. Seasonal variations in nearshore circulation in the northwestern Gulf of Mexico. Contrib. Mar. Sci. 19:49-65.
SWINGLE, H. A., AND D. G. BLAND.
1974. A study of the fishes of the coastal watercourses of Alabama. Ala. Mar. Res. Bull. 10:17-102.
TABB, D. C.
1961. A contribution to the biology of the spotted seatrout, *Cynoscion nebulosus* (Cuvier) of east-central Florida. Fla. Board Conserv., Mar. Resour. Lab. Tech. Ser. 35, 24 p.
TAYLOR, H. F.
1916. The structure and growth of the scales of the squeteague and the pigfish as indicative of life history. Bull. U.S. Bur. Fish. 34:285-330.
TESCH, F. W.
1971. Age and growth. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, 2d ed., p. 98-126. Blackwell Sci. Publ., Oxf.
THOMAS, D. L.
1971. The early life history and ecology of six species of drum (Sciaenidae) in the lower Delaware River, a brackish tidal estuary. Ichthyol. Assoc. Bull. 3, 247 p.
TRENT, L., AND P. J. PRISTAS.
1977. Selectivity of gill nets on estuarine and coastal fishes from St. Andrew Bay, Florida. Fish. Bull., U.S. 75:185-198.
VICK, N. G.
1964. The marine ichthyofauna of St. Andrew Bay, Florida, and nearshore habitats of the northeastern Gulf of Mexico. Tex. A&M Univ. Res. Found. A&M Proj. 286-D, 77 p.
WALLACE, D. H.
1940. Sexual development of the croaker, *Micropogon undulatus*, and distribution of the early stages in Chesapeake Bay. Trans. Am. Fish. Soc. 70:475-482.
WEINSTEIN, M. P., AND R. W. YERGER.
1976. Protein taxonomy of the Gulf of Mexico and Atlantic Ocean seatrouts, genus *Cynoscion*. Fish. Bull., U.S. 74:599-607.

WELSH, W. W., AND C. M. BREDER, JR.
1923. Contributions to life histories of Sciaenidae of the eastern United States coast. Bull. U.S. Bur. Fish. 39:141-201.

WHITE, M. L., AND M. E. CHITTENDEN, JR.
1977. Age determination, reproduction, and population dynamics of the Atlantic croaker, *Micropogonias undulatus*. Fish. Bull., U.S. 75:109-123.

WILK, S. J.
1979. Biological and fisheries data on weakfish, *Cynoscion regalis* (Bloch and Schneider). U.S. Dep. Commer., NOAA, NMFS, Sandy Hook Lab., Tech. Ser. Rep. 21, 49 p.

WOLFF, M.
1972. A study of North Carolina scrap fishery. N.C. Dep. Nat. Econ. Resour., Div. Comm. Sport Fish., Spec. Sci. Rep. 20, 29 p.

MOVEMENTS AND ACTIVITIES OF THE ATLANTIC BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS*, NEAR SARASOTA, FLORIDA

A. BLAIR IRVINE,[1] MICHAEL D. SCOTT,[2] RANDALL S. WELLS,[3] AND JOHN H. KAUFMANN[4]

ABSTRACT

A tagging-observation program was conducted to study the behavioral ecology of Atlantic bottlenose dolphins near Sarasota, Florida. Forty-seven bottlenose dolphins (24 males, 23 females) were captured, tagged, and released a total of 90 times from 29 January 1975 through 25 July 1976. Tagged animals were identified during regular boat surveys, and information was collected on all individuals and groups encountered. A total of 997 tagged or marked bottlenose dolphins were sighted. A population of bottlenose dolphins was identified in an estuarine-nearshore area extending about 40 km to the south from Tampa Bay and up to 3 km into the Gulf of Mexico. Social organization was characterized by small dynamic groups that appeared to be subunits of a larger socially interacting herd. Average group size of 688 groups was 4.8 bottlenose dolphins (standard error = 0.16). Bottlenose dolphins concentrated in different areas seasonally, possibly in response to distribution changes of important prey species. Feeding strategies of the bottlenose dolphins apparently varied according to available water depth and differed from strategies of pelagic small cetaceans. Calving apparently occurred from spring to early fall.

Until the 1970's, information on the natural history of free-ranging small cetaceans consisted primarily of chance observations (e.g., Norris and Prescott 1961). Increased interest and application of new technology have now greatly expanded our knowledge. Long-term studies of the behavior and ecology of dolphins have been conducted by researchers using boats, submersibles, aircraft, and towers or cliff-top vantage points (see review by Norris and Dohl 1980a). Biotelemetry and newly developed tagging techniques have been used extensively to gather information on delphinid movements, activities, and herd structure (Norris and Pryor 1970; Evans et al. 1971; Perrin 1975; Leatherwood and Evans 1979; Norris and Dohl 1980b). Natural marks that identify individuals have also been used as the basis for field studies of dolphins (Würsig and Würsig 1977, 1979; Shane and Schmidly[5]) as well as whales (Pike 1953; Payne 1976; Katona et al. 1979; Balcomb and Goebel[6]). Unfortunately, in most studies of free-ranging cetaceans, the age, size, and sex of herd members was usually unknown, and consequently few details about herd structure and social dynamics were collected.

The research reported here was an 18-mo tagging-observation study to collect data on movements, home range, herd structure, and habitat use of the bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Fla. (lat. 27°25′ N, long. 80°40′ W). This area was chosen for several reasons: bottlenose dolphins were present throughout the year in areas where channels and islands limited their movements to predictable routes (Irvine and Wells 1972); because the area was used by many boaters, discrete use of an observation boat was not likely to affect the bottlenose dolphins' behavior; and mild weather and sheltered waters made year-round observations feasible. The study was intended to provide insights into the ecology of bottlenose dolphins in a bay-estuarine environment. This report is a revision and reanalysis of parts of Irvine et al.[7]; Wells et al. (1980)

[1]Gainesville Field Station, Denver Wildlife Research Center, 412 NE 16th Avenue, Gainesville, FL 32601.
[2]Department of Zoology, University of Florida, Gainesville, Fla.; present address: Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92037.
[3]Department of Zoology, University of Florida, Gainesville, Fla.; present address: Center for Coastal Marine Studies, University of California, Santa Cruz, CA 95064.
[4]Department of Zoology, University of Florida, Gainesville, FL 32611.
[5]Shane, S. H., and D. J. Schmidly. 1978. The population biology of the Atlantic bottlenose dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PB-283 393, 130 p.

Manuscript accepted June 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

[6]Balcomb, K. C., III, and C.A. Goebel. 1976. A killer whale study in Puget Sound. Final Report to the National Marine Fisheries Service, Contract No. NASO-6-35330. Unpubl. rep.
[7]Irvine, A. B., M. D. Scott, R. S. Wells, J. H. Kaufmann, and W. E. Evans. 1979. Appendix A, A study of the activities and movements of the Atlantic bottlenose dolphin, *Tursiops truncatus*, including an evaluation of tagging techniques. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PB-298 042, 54 p.

present an in-depth analysis of social behavior data from the same study.

METHODS

Study Area

The study area included inshore and coastal waters up to 3 km off the coast, extending about 40 km south from the southern edge of Tampa Bay, Fla. This area is characterized by bays and grass flats 1-4 m deep, and is protected by a series of barrier islands separated by narrow passes (Figure 1). Inshore waters, defined here as the waters between the barrier islands and the mainland, were generally protected from heavy winds and ocean swells. The Intracoastal Waterway (ICW), a boat channel between the barrier islands and the mainland, is maintained by dredging to depths of at least 2 or 3 m. Depths in the Gulf of Mexico increase gradually; the 10 m contour is about 3 km offshore (N.O.S. Chart No. 11425).

Data Collection and Analysis

We captured bottlenose dolphins using the seine net technique described by Asper (1975). We recorded the length and sex of all captured animals and then marked them with combinations of spaghetti tags, fiber glass "visual" tags, freeze brands, roto tags, and radio tags, using methods developed and tested on other small cetaceans (Norris and Pryor 1970; Evans et al. 1972). The radio tags were modified dolphin transmitters, model PT 219, of the Ocean Applied Research Corporation (OAR[8]). Transmitter signals were received on an OAR model 210 Auto-

[8]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

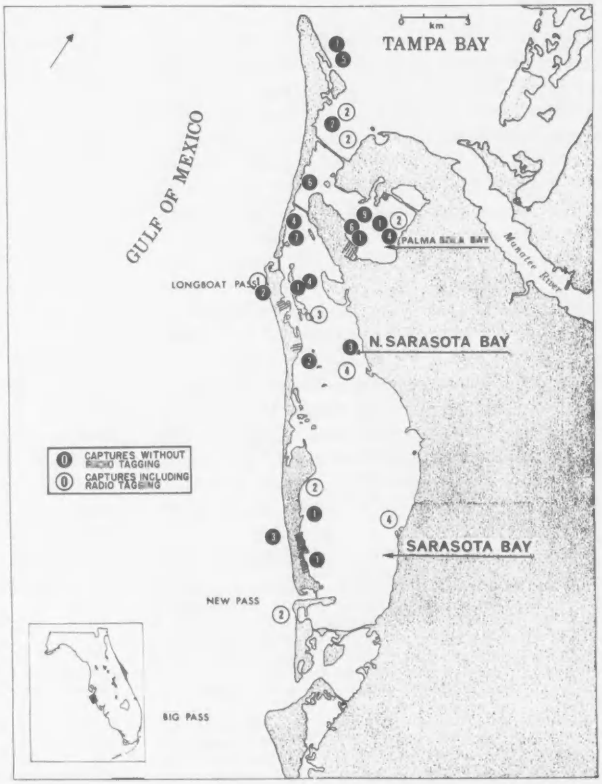

FIGURE 1.—The study area, located south of Tampa Bay near Sarasota (lat. 27°25′ N; long. 80°40′ W), Fla. The encircled numbers indicate numbers of bottlenose dolphins captured at each site.

matic Direction Finder. The tags and marking techniques used in the study were described and evaluated by Irvine et al. (footnote 7).

The boat used as a tagging platform and for surveys and radio tracking was a 7.3 m Wellcraft "Fisherman," equipped with a 3 m tuna tower. During captures, the boat was camouflaged with canvas and netting and towed to the capture site to lessen chances that tagged bottlenose dolphins might later recognize the motor sounds or visually identify the boat, and avoid it during surveys.

Radio-tagged bottlenose dolphins were usually tracked continuously for 24-48 h after installation of the radio transmitter and then relocated and tracked intermittently during the remaining life of the transmitter. As reported by Martin et al. (1971), the radio tags transmitted only when the antenna was at the surface, enabling us to measure dive times by timing the intervals between transmissions. Tracking was generally conducted from a distance and at anchor, to lessen possible influences of the tracking boat on the bottlenose dolphins' movements. Locations of radio tagged animals were determined at night by triangulation and during the day by triangulation or occasional sightings.

Boat surveys were conducted during periods when bottlenose dolphins were not being radio tracked. Surveys were conducted at least twice a week and were concentrated in northern inshore areas (Figure 2). Surveys were extended to include the Gulf of Mexico and southern inshore areas when time was allowed. Survey routes were influenced by tide and wind but were usually confined to channels or other areas >1 m deep (Figure 2).

During boat surveys and tracking trips, all dolphins sighted were counted, and tagged or marked individuals were identified if possible. Groups containing several recognizable animals were usually observed for longer periods to verify identities and associations. The distribution of sightings was therefore influenced by boat channels and by the length of time that groups were followed.

The location and direction of movement of all bottlenose dolphins sighted were noted on charts, and notes on each encounter were entered on data sheets. To correct for repeated sightings of known individuals during the same survey, we based distribution and herd size analyses on sightings more than 1 h apart. Associations between recognizable bottlenose dolphins were compiled as one sighting per group per day, but were retabulated each time the composition of a group changed. For "seasonal" analysis, the year was divided into quarters based on the beginning of field activities (29 January 1975) as follows: February, March, and April (spring); May, June, and July (summer); August, September, and October (fall); and November, December, and January (winter).

Population units were difficult to define because sea conditions and local topography usually limited sightings to nearby animals. Consequently, all bottlenose dolphins sighted within about 100 m of the boat were defined as a group. The smallest group of bottlenose dolphins observed to be closely associating and engaging in similar activities was labeled a primary group. Combinations of primary groups were labeled secondary groups. A "herd" was defined as an aggregation of bottlenose dolphins that more or less regularly occupied a given area and interacted socially with each other to a markedly greater extent than with bottlenose dolphins in adjacent areas. This definition of a herd was based on observed social interactions or associations over an extended period of time. At any given time, the members of the herd were distributed among a number of primary and secondary groups. Herds sighted during aerial surveys (e.g., Leatherwood et al. 1978) have been defined, by necessity, by proximity of animals sighted, and are probably most comparable to our definitions of primary and secondary groups.

RESULTS AND DISCUSSION

Forty-seven bottlenose dolphins (24 males, 23 females) were captured or recaptured for tagging a total of 90 times between 29 January 1975 through 25 July 1976. Ten dolphins (designated RT-1 to RT-10) were fitted with radio tags and radio tracked for up to 22 d. The total of 3,331 bottlenose dolphins sighted (Figure 3) included 2,373 during surveys (730.2 h), 529 during radio tracks (245.3 h), and 429 during capture efforts (150.8 h). Of the 997 marked bottlenose dolphins that were sighted, 781 were tagged and identifiable, 129 were tagged but unidentifiable, and 87 (distributed among 12 dolphins) were identifiable by distinctive natural marks (usually dorsal fin shape). Numerous sightings from close range suggested that tagged bottlenose dolphins did not attempt to avoid the tagging-observation boat.

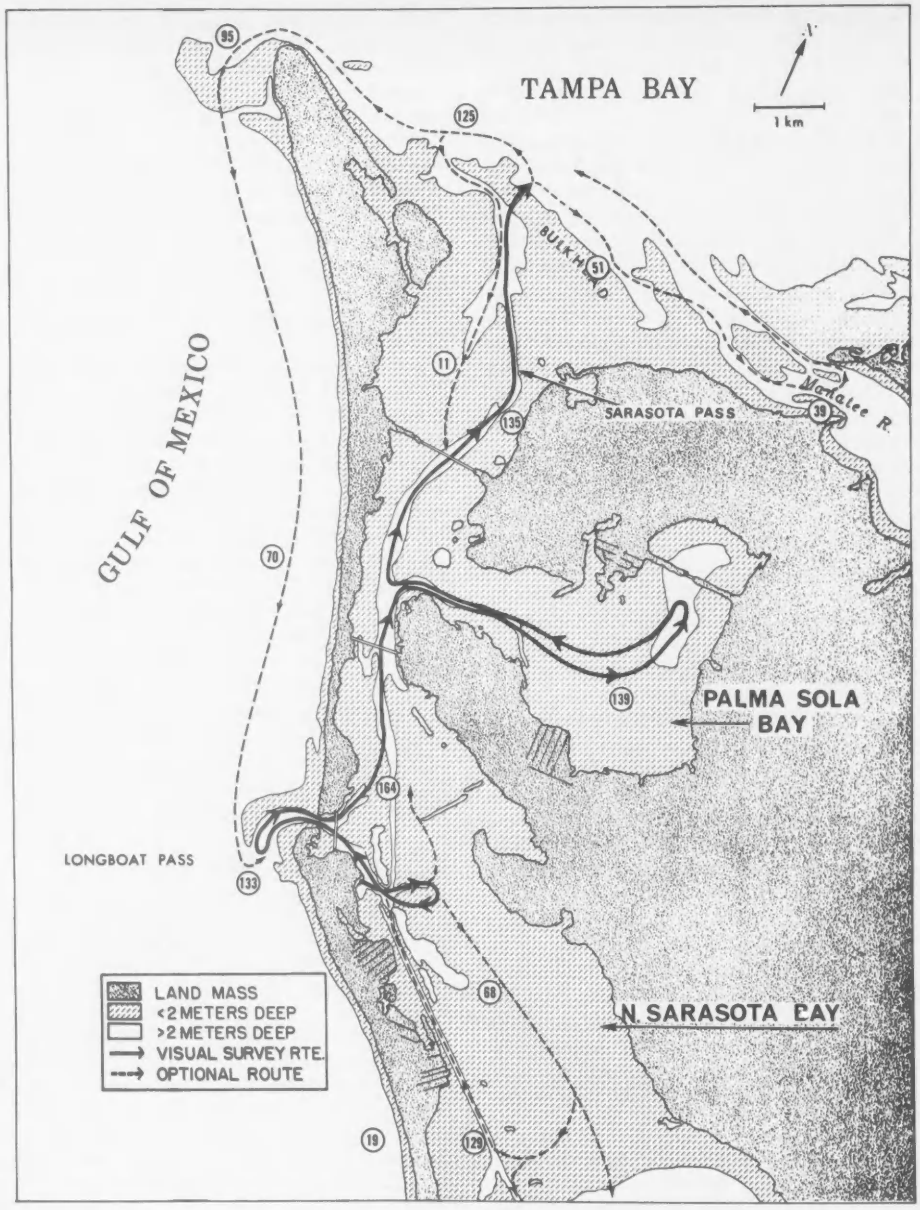

FIGURE 2.—Northern part of the study area with numerals indicating number of surveys along specific routes. Solid lines indicate usual routes. Dashed lines indicate optional routes taken when weather and time permitted. Tagged bottlenose dolphins often traveled north to the edge of Tampa (solid line route) before turning east or west (dashed line) or returning south.

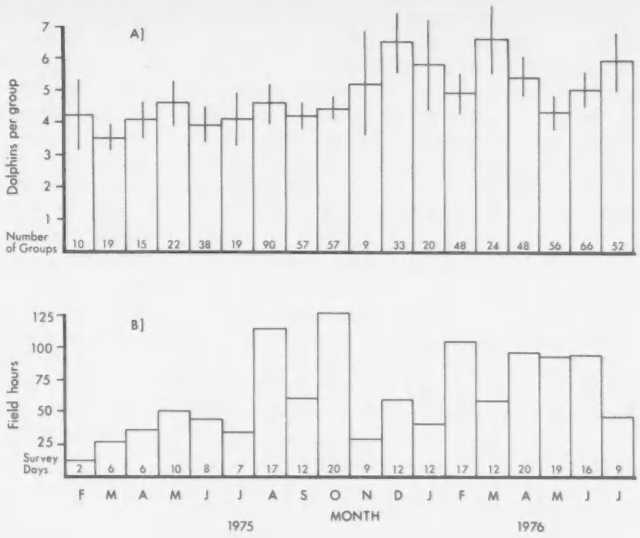
A]
Dolphins per group
Number of Groups
10 19 15 22 38 19 90 57 57 9 33 20 48 24 48 56 66 52
B]
Field hours
Survey Days
2 6 6 10 8 7 17 12 20 9 12 12 17 12 20 19 16 9
F M A M J J A S O N D J F M A M J J
MONTH
1975
1976

FIGURE 3.—Compilation of bottlenose dolphin sighting data by month, from boat surveys: A) Average number of dolphins sighted per group with standard error (vertical lines) and numbers of groups sighted (numerals) for each month. B) Number of field hours and boat survey days (numerals).

Home Range

Resightings of tagged bottlenose dolphins suggest that at least some were year-round residents of the study area (Figure 4). We recaptured 11 of the 12 animals tagged in 1970-71 by Irvine and Wells (1972) and identified them by freezebrands, tag scars, or dorsal fin shape—strongly implying that some bottlenose dolphins may remain in the area for several years. The existence of resident bottlenose dolphins has previously been widely proposed (Caldwell 1955; Caldwell and Golley 1965; Norris and Pryor 1970; Saayman et al. 1972; Saayman et al. 1973; Würsig and Würsig 1977, 1979; Würsig 1978; Saayman and Tayler 1979; Norris and Dohl 1980b; Shane and Schmidly footnote 5).

The home range of the bottlenose dolphins in the study area appeared to extend south from the southern edge of Tampa Bay to Big Pass (Figure 5; see also Wells et al. 1980), and to include inshore areas and waters up to 1 km into the Gulf of Mexico. No tagged bottlenose dolphins were observed more than 1 km offshore; however, survey trips rarely extended farther than 3 km offshore. At their apparent northern boundary, tagged animals terminated northerly movements at the edge of Tampa Bay by turning either east or west (Figure 2). Groups containing identifiable naturally marked bottlenose dolphins, apparently

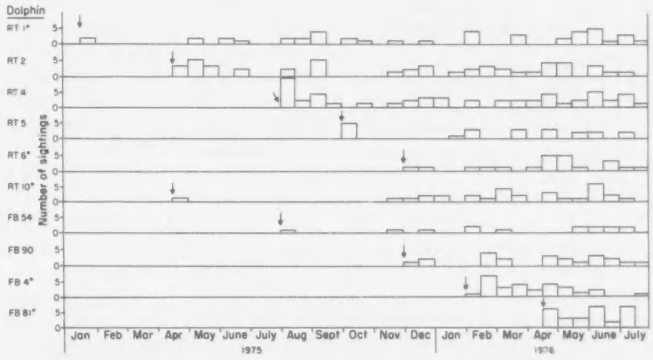

FIGURE 4.—Total biweekly sightings of selected tagged bottlenose dolphins; one sighting per day included. Twenty-three of these sightings were reported by other observers. Arrows indicate capture dates. Sighting locations of dolphins marked with an asterisk are shown in Figure 5.

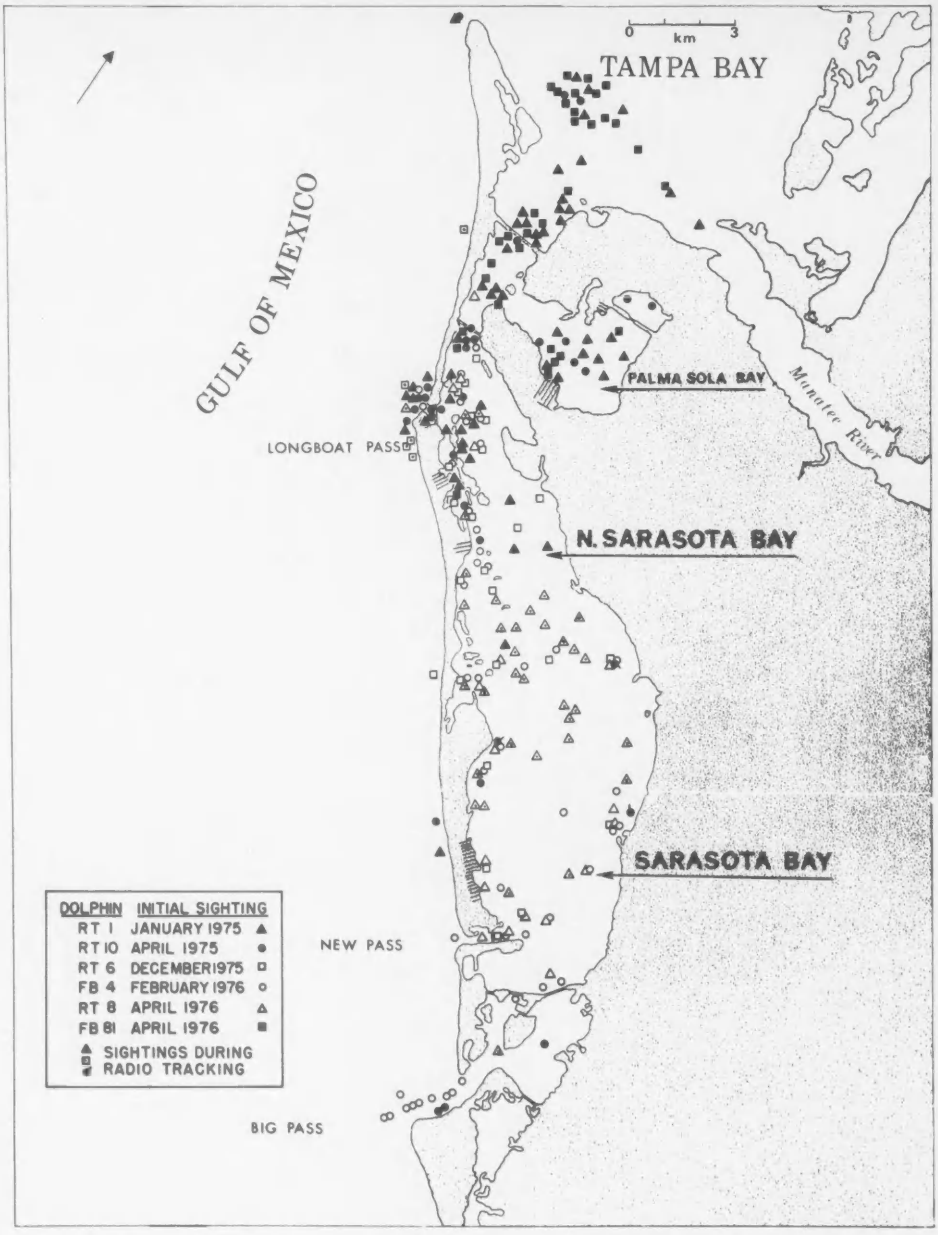

FIGURE 5.—Locations of accumulated sightings of six marked bottlenose dolphins. Sightings of these dolphins were selected to demonstrate generalized use of northern or southern parts of the study area by some animals. The home range of all tagged bottlenose dolphins in the study area extended from approximately southern Tampa Bay to Big Pass.

not belonging to the study herd, occasionally moved along the southern edge of Tampa Bay, but rarely approached tagged bottlenose dolphins and were never observed moving south in the ICW. The only tagged bottlenose dolphins known to have left the study area were two radio-tagged animals that left briefly (one moved 15 km north, the other 10 km south) on the first night after tagging. Both returned within 10 h.

The home range boundary cues used by the animals are unknown. At Tampa Bay, bottlenose dolphins might have used acoustic or visual cues associated with the sharp dropoff at the edge of Tampa Bay. Bottlenose dolphins may use landmarks to limit movements in Golfo San Jose, Argentina (Würsig and Würsig 1979), although known individuals also disappeared from the study area for 6 mo, were resighted 300 km away and then were rediscovered back in the study area 9 mo later (Würsig and Würsig 1977). Long-range movements by some group members but not by others have not been reported elsewhere; however, most studies of bottlenose dolphin home range have been conducted in restricted geographical areas with relatively few identifiable animals (see review by Norris and Dohl 1980a).

Movements and Activities

Movement patterns were similar throughout the northern part of the study area. Slow moving groups of up to six animals often spent several hours over grass flats 1-3 m deep, particularly west of the ICW north of Sarasota Pass and east of the ICW in northern Sarasota Bay (Figure 2).These groups were usually dispersed and dynamic; individuals often approached each other only occasionally, but all usually moved in the same general direction. The pace of individuals quickened at irregular intervals when apparent feeding occurred. Typically, a group of bottlenose dolphins was found in one part of the study area for several survey days, before it moved to another area, but locations and intragroup associations were generally not predictable.

Group members often converged and used channels to move between areas, usually at speeds of 2-5 km/h, although occasionally small groups in tight formation moved along the ICW at speeds exceeding 5 km/h. North-south movements of up to 30 km in a day have been observed but were not typical.

Bottlenose dolphin distribution, and perhaps abundance, differed seasonally within the home range (Figure 6). In winter, bottlenose dolphins were most abundant in passes and along the gulf shore, whereas during the warmer months relatively higher numbers were sighted in the channels and bays inshore of the barrier islands. These localized changes in bottlenose dolphin distribution may reflect changes in the distribution of food resources, or possibly seasonal changes in abundance of sharks (Wells et al. 1980).

Unlike the habitat of pelagic cetaceans, which theoretically does not restrict horizontal and vertical movements, the shallowness of many parts of our study area restricted vertical movements and thereby dictated bottlenose dolphin travel routes and influenced the structure of swimming groups. Bottlenose dolphins were only occasionally observed crossing areas <1 m deep. Bottlenose dolphins have partly beached themselves in Georgia marshes while pursuing fish (Hoese 1971), and other dolphins have been observed feeding in estimated depths of <50 cm (A. B. Irvine pers. obs.; J. S. Leatherwood[9]).

The habitat used by the bottlenose dolphins reported here appears most like that of the humpback dolphin, *Sousa* sp., observed from cliffs in South Africa (Saayman et al. 1972; Tayler and Saayman 1972; Saayman and Tayler 1973, 1979; Saayman et al. 1973) and bottlenose dolphins observed in a bay in Argentina (Würsig and Würsig 1977, 1979; Würsig 1978). In these areas, the animals also usually moved in small groups and fed individually. Although most bottlenose dolphin sightings in our study area were east of the barrier islands, tagged animals were also periodically observed near shore in the Gulf of Mexico. Bottlenose dolphins are found from well offshore into extreme shallows in the Gulf of Mexico (Leatherwood 1975; Leatherwood et al. 1978; Odell and Reynolds[10])—suggesting a distribution that is similar to that of bottlenose dolphins studied in South Africa (Saayman et al. 1972; Tayler and Saayman 1972; Saayman and Tayler 1973, 1979; Saayman et al. 1973).

Movements of bottlenose dolphins with the tides were suggested by True (1885), Gunter (1942), Irvine and Wells (1972), Würsig and Würsig

[9]S. Leatherwood, research biologist, Hubbs-Sea World Research Institute, San Diego, CA 92109, pers. commun. March 1980.

[10]Odell, D. K., and J. E. Reynolds. 1980. III, Distribution and abundance of the bottlenose dolphin, *Tursiops truncatus*, on the west coast of Florida. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PB 80-197 650, 47 p.

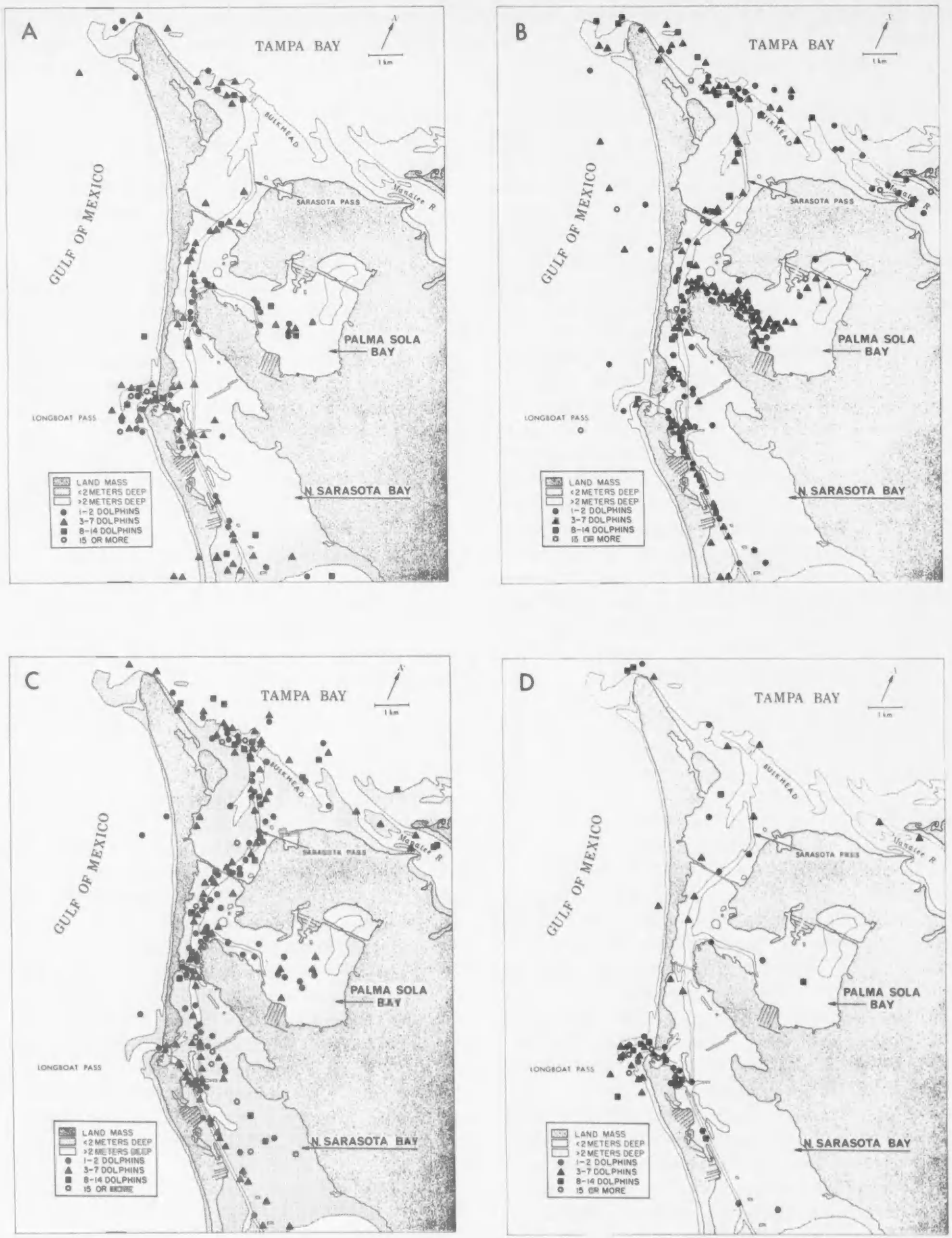

FIGURE 6.—Locations of bottlenose dolphins sighted during 3-mo periods: A) February, March, and April 1975 and 1976; B) May, June, and July 1975 and 1976; C) August, September, and October 1975; D) January, November, and December 1975, and January 1976.

(1979); however, Shane (1980) reported more movements against than with the tidal current, and Leatherwood (1979) reported seeing no relation between the bottlenose dolphin movements and tide. As indicated in Figure 7, considerably more bottlenose dolphins in our study were moving with than against the tidal currents, although the numbers of groups moving with and against the currents were almost equal. This observation suggests that larger groups of animals more often moved with the tide. The data were not analyzed statistically because a large number of animals seen were in the "milling" category, moving across the current or in irregular patterns.

The tidal current in the study area varied with physiography, but was strongest in narrow channels and passes, at times exceding 5 km/h. In Palma Sola Bay, a shallow bay with one access channel, bottlenose dolphins more often moved against than with a sometimes strong current. The animals rarely reversed direction in the Palma Sola Bay channel but often swam near the sides of the channel possibly because current velocity was reduced there.

Movement and activity patterns were not influenced by other environmental conditions in any recognizable way. Possible sun orientation, as reported for the common dolphin, *Delphinus delphis*, by Pilleri and Knuckey (1968) and Evans (1971), was not observed, although the restrictions of movements dictated by area physiography may have masked such effects. We did not detect the distinctive day-night dive interval patterns noted for other dolphin species by Evans (1971, 1974, 1975), Leatherwood and Evans (1979), Leatherwood and Ljungblad (1979), Norris and Dohl (1980b), and Würsig (in press, see footnote 11).

Social Structure

Available evidence suggests that the study area was occupied by a single discrete social unit or "herd." Groups containing naturally marked bottlenose dolphins that were seemingly not a part of this herd were repeatedly observed north, west, and south of the study area. These observations suggest that the bottlenose dolphin population on Florida's west coast may be composed of a number of distinct herds inhabiting limited geographical areas. Overlapping home ranges have also been proposed for coastal bottlenose dolphins off southern California (Leatherwood and Reeves 1978).

The uneven dispersal of sightings of bottlenose dolphins of different age and sex classes within the

[11] Würsig, B. 1976. Radio tracking of dusky porpoises (*Lagenorhynchus obscurus*) in the South Atlantic, a preliminary analysis. ACMRR Scientific Consultation on Marine Mammals, Bergen, Norway, 21 p.

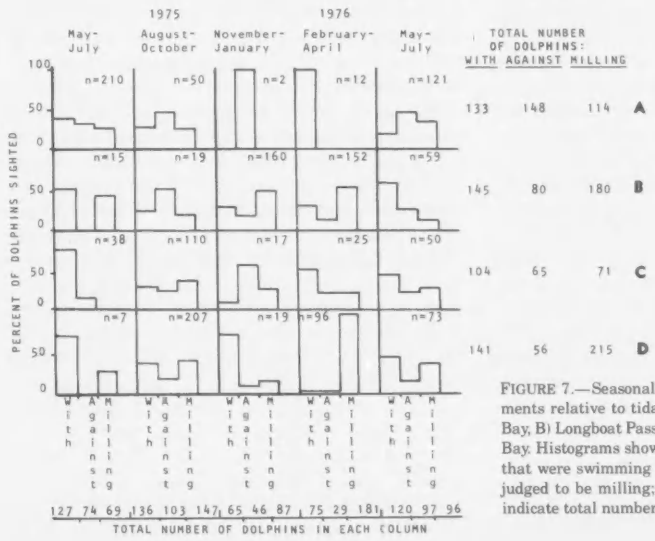

FIGURE 7.—Seasonal relationship of bottlenose dolphin movements relative to tidal flow in selected areas. A) Palma Sola Bay, B) Longboat Pass, C) Sarasota Pass, and D) North Sarasota Bay. Histograms show percent of dolphins sighted in each area that were swimming with the current, against the current, or judged to be milling; the numbers in each category and area indicate total number of dolphins seen.

study area suggested the presence of several "subherds" (Figure 5). The bulk of the tag sightings in the southern part of the study area were of the same subadult male groups, whereas cow-calf pairs were more commonly sighted in the north (Wells et al. 1980). However, some identifiable bottlenose dolphins were sighted in all parts of the study area and were associated with as many as 20 other tagged animals. Overall, we interpret the resightings of tagged animals to indicate that different age and sex classes may have favored different areas, but that social relationships were still maintained among members of the entire herd.

Bottlenose dolphins from adjacent areas that occasionally approached animals from the study herd remained for only a few minutes, and social interactions between the different groups were not observed. Various species of macropods, primates, and ungulates have similar social organizations; subgroups join to form discrete social units ("mobs," "troops," or "herds") that exhibit spatial fidelity and have little interaction with conspecifics outside the social unit (see review by Wilson 1975).

The size of the herd within the study area was difficult to determine. Boat survey results were variable, and information on bottlenose dolphin migration was unavailable. However, the lack of sightings from outside the study area, the observed movements of visually and radio-tagged dolphins, and an increase in tag sightings as the number of tags installed increased (Table 1) all suggested that the captures involved a discrete population of bottlenose dolphins. Assuming a constant population size with no emigration or immigration, we estimated that the local population contained 102 bottlenose dolphins (95% confidence limits = 90-117), using a Lincoln Index (Overton 1971) and a basis of 35 survey days (165 h), from 9 May through 9 July 1976 (Table 1). Until more data are available about this assumption, however, our population estimate must be viewed with caution.

Assuming that the group home range was 85 km^2 (Wells et al. 1980), the estimated population size suggests a density of 1.3 bottlenose dolphins/km^2. Aerial surveys indicate densities of 0.23-0.68 bottlenose dolphin/km^2 in other coastal areas of the southeastern United States (see review by Leatherwood 1979). Monthly mean bottlenose dolphin densities derived from surface survey data of Shane (1980) were 1.5-5.1 bottlenose dolphins/km^2 near Port Aransas, Tex., whereas aerial density estimates at the same area were 2.6 bottlenose dolphins/km^2 (Barham et al. 1980). The reasons for the large discrepancies between aerial and surface survey density estimates are unclear. Some animals may be counted more than once from boats, or perhaps observers in rapidly moving aircraft do not see all bottlenose dolphin groups. In any case, the differences in density estimates suggest that population estimates of bottlenose dolphins in Florida based on aerial and surface surveys may not be directly comparable.

It is not known whether the study herd remained intact throughout the year or changed composition seasonally. Tagged bottlenose dolphins that were not sighted for long periods (see Figure 4) may have lost their identifying tags, or may have left the study area, as did some bottlenose dolphins in Argentina (Würsig and Würsig 1977).

Fewer than 15% of the field sightings were of solitary bottlenose dolphins, which is an indication of the high degree of gregariousness of free-ranging bottlenose dolphins (Figure 8). Average group size (n = 688 groups) varied from 2 to 6 about an overall mean of 4.8 bottlenose dolphins/group (SE = 0.16; Figures 3A, 8). During summer 1975 and early summer 1976, groups of >40 unmarked bottlenose dolphins, probably from adjacent herds, were observed <1 km offshore in the Gulf of Mexico and within 1 km of the northern

TABLE 1.—Sightings of marked and unmarked dolphins and population size estimates, during periods from December 1975 to July 1976.

Item	17 Dec.-13 Feb.	15 Feb.-17 Mar.	20 Mar.-14 Apr.	17 Apr.-6 May	9 May-6 June	12 June-9 July
A) Number of marked dolphins	19	[1]20.75	24	[1]27.83	37	38
B) Total number of dolphins sighted	261	176	49	200	226	[2]415
C) Number of marked dolphins sighted	38	49	10	67	103	132
D) C/B	0.15	0.28	0.20	0.34	0.46	0.32
E) Estimated population size	130	74	118	83	81	119
F) 95% confidence limits	91-179	55-98	55-221	65-106	67-99	100-142

[1]Tagged dolphins were found dead on 5 March and 3 May 1976; population estimates are adjusted to account for survey days after these animals were dead.
[2]Includes 95 unmarked dolphins (in 5 groups) sighted on the periphery of the study area.

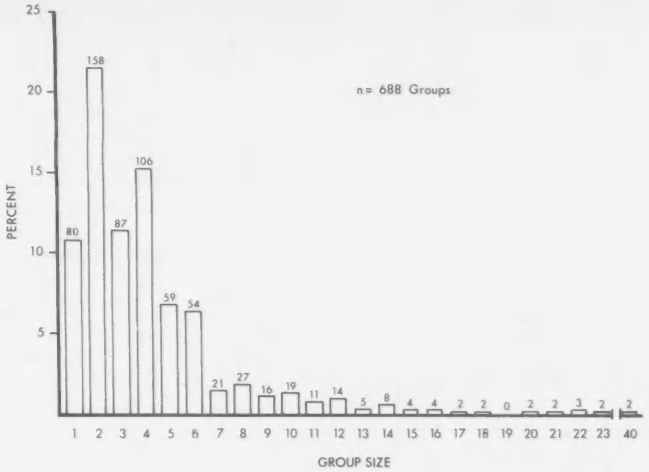

FIGURE 8.—Group size-frequency distribution. Groups were defined as all animals within about 100 m of the survey boat. Numerals indicate the number of groups in each size category.

limit of the study area in Tampa Bay. However, group size-frequency distributions did not vary significantly by month ($P>0.60$; chi-square) or season ($P>0.90$; chi-square). Group sizes were not normally distributed (Kolmogorov-Smirnov test; $P>0.05$) during 11 of the 18 mo of field activity (518 sightings), even after square root transformations (Sokal and Rohlf 1969). The lack of significant monthly trends in herd size was corroborated ($P\leq0.35$) by a Kruskal-Wallis nonparametric analysis of variance test (Sokal and Rohlf 1969).

Social Interactions

Applying the body length-maturity relationship of Sergeant et al. (1973) we categorized each tagged bottlenose dolphin as adult or subadult. The frequencies of interactions between bottlenose dolphins of various age and sex categories are summarized in Figure 9. Adult males (246-268 cm long) associated primarily with females, apparently preferring females without calves, and were rarely observed with subadult males (210-237 cm). Subadult males were most often seen together. Adult females (235-250 cm) were sighted most often with other females. Subadult females (207-234 cm) were also frequently associated with adult females. An adult female nicknamed "Killer" (240 cm long) was usually sighted with subadult males or four adult females. Details of these observed associations are also discussed by Wells (1978) and Wells et al. (1980).

Sexually segregated groups were sighted on a number of occasions in our study and have been reported in other studies (Evans and Bastian 1969; D. K. Caldwell and M. C. Caldwell 1972; Irvine and Wells 1972; Tayler and Saayman 1972; Mead 1975; Norris and Dohl 1980a). Tavolga (1966) noted four subgroups in her detailed study of a captive colony of bottlenose dolphins at Marineland of Florida: a single adult male, adult females, subadults (mostly males), and juveniles. Miyazaki and Nishiwaki (1978) classified groups of the striped dolphin, *Stenella coeruleoalba*, into juvenile, mature mating, and mature nonmating schools, but did not report if sexual isolation occurred. Tayler and Saayman (1972) reported on the basis of five captures that subadult male bottlenose dolphins off South Africa are rarely found with "bulls" or in exclusively subadult male groups, but that captive subadult males do closely associate with bulls.

Our observations suggest that subadult males rarely interacted with bulls, but largely formed stable primary groups among themselves. Subadult males were never captured with adult males (28 captures). We observed apparent homosexual interactions within a primary group of four known subadult males during February to July 1976, but cannot verify if it is a year-round behavior. Behaviors were classified as homosexual only when an extruded penis or an apparent copulatory attempt was observed.

"Killer's" frequent association with subadult males is difficult to explain. Inasmuch as she was

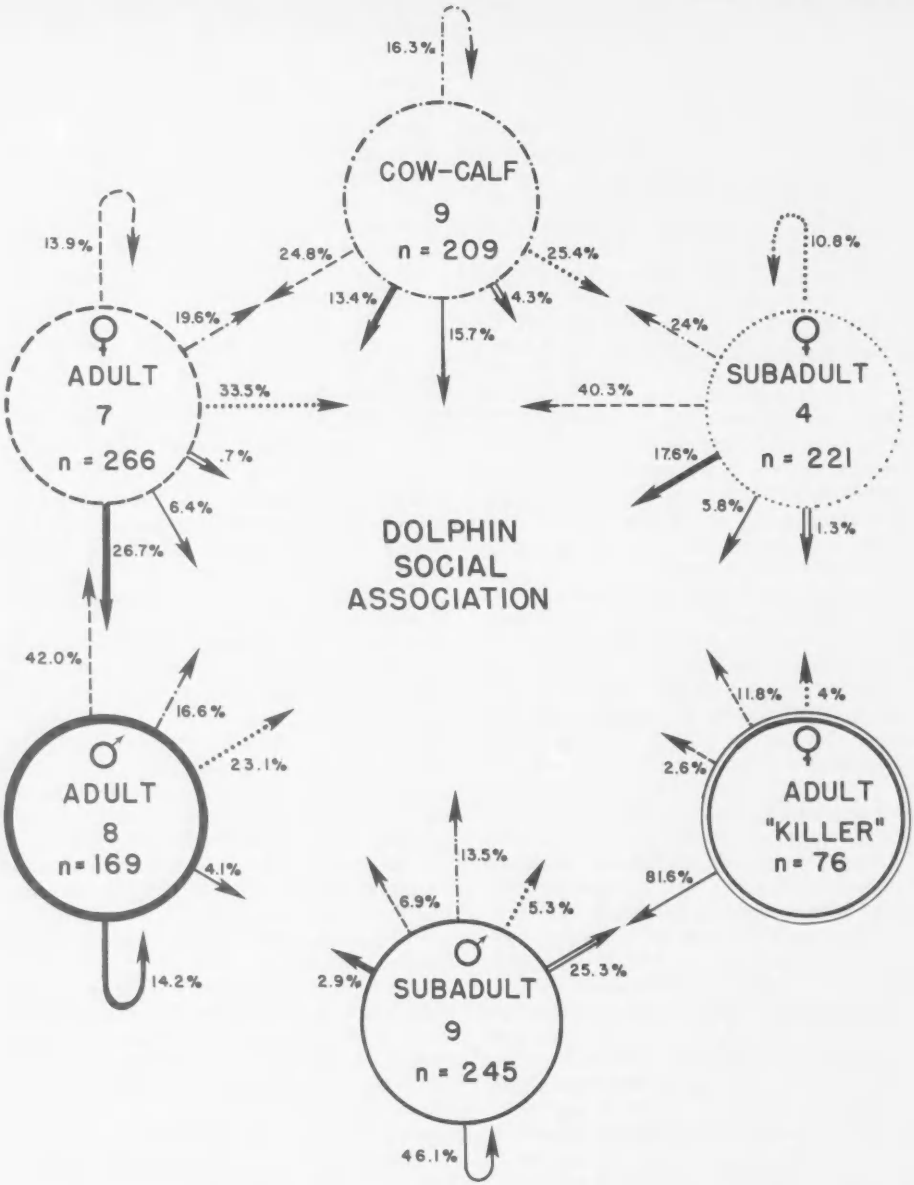

FIGURE 9.—Component social interactions among age-sex classes of known bottlenose dolphins. Sex and length were determined when the animals were captured. Age classes are based on body length-maturity data from Sergeant et al. (1973). Number of individuals is presented under each age-class. n = number of observations. Adult female "Killer" was a dolphin that had an atypical association pattern (see text).

captured and sexed several times, error in sex determination is not likely. She was occasionally seen with the same group of subadult males that had been observed engaging in homosexual activities, and on one occasion she appeared to engage in sexual activities with at least one member of that group.

The associations of longest duration involved cows and calves, although relatively prolonged aggregations of subadult males and frequent associations of adult males with adult females were noted in the spring. One calf was observed during 30 of 32 sightings of the apparent mother over a period of 15 mo, and another calf was observed with its mother on all of 20 sightings during a 9-mo period. We did not observe straying of calves, as has been noted in captivity (see review by M. C. Caldwell and D. K. Caldwell 1972) and inferred for free-ranging bottlenose dolphins in Argentina (Würsig 1978) and the Gulf of Mexico (Leatherwood[12]).

When pursued during capture attempts, calves stayed close beside their fleeing mothers, apparently being partly pulled along in the suction created by the mother's movement through the water (Norris and Prescott 1961; Norris and Dohl 1980a; Leatherwood footnote 12). While the mother was being tagged, calves remained close to the stretcher, often emitting underwater whistles audible in air. A calf released outside the net quickly became tangled in the net while attempting to return inside, where its mother was trapped. When a cow was released before her calf was freed, she invariably patroled outside the net until the calf was released. On one occasion a loud whistle from a bottlenose dolphin calf being tagged brought the mother rapidly to within 5 m of the capture net from a point about 75 m away. Apparently similar behaviors have been observed for *Stenella* sp. involved in the purse seine fishery for yellowfin tuna, *Thunnus albacares* (W. F. Perrin[13]). Close approaches by large male killer whales, *Orcinus orca*, to the outside of an enclosure containing a killer whale calf have also been observed by A. B. Irvine in Puget Sound.

Dolphins being pursued by the capture boat fled as a close-knit group often in a line abreast formation. As with bottlenose dolphins off California (Norris and Prescott 1961; Norris and Dohl 1980a) and off Louisiana (Leatherwood and Platter[14]), some bottlenose dolphins recognized the capture boat and began fleeing rapidly 400 m or more ahead of the boat. The bottlenose dolphins apparently associated the sound of the boat's engine with past captures, since naturally marked animals not previously subjected to our capture attempts did not flee. When part of a bottlenose dolphin group was encircled, the remaining members did not temporarily remain nearby, as has been reported for *Steno bredanensis* (Evans 1967), common dolphins (Pilleri and Knuckey 1968), the dusky dolphin, *Lagenorhynchus obscurus* (Würsig and Würsig 1980), and killer whales (Balcomb and Goebel footnote 6). We often observed and sometimes recaptured dolphins near earlier capture sites, suggesting that capture areas were not avoided.

Behaviors associated with the formation and maintenance of intragroup associations are not well understood. Studies of captive animals have indicated that dominance, exerted by combinations of physical posturing, aggression, and vocalization, may be important in the establishment and maintenance of social hierarchies (Tavolga 1966; M. C. Caldwell and D. K. Caldwell 1967, 1972; Evans and Bastian 1969). Most studies of captive dolphins, however, have been of <15 dolphins, often interspecifically mixed, and confined in a tank. The dominance hierarchies and social structure described for captive groups may therefore not represent the social organization of free-ranging bottlenose dolphins. For instance, the concept of microterritories suggested for captives (M. C. Caldwell and D. K. Caldwell 1972; Tayler and Saayman 1972) and presumably maintained by dominance relationships is probably not relevant to the study of wild bottlenose dolphins, which move constantly and change companions often. The small "family unit" concept proposed by McBride and Kritzler (1951) is also not compatible with our observations of dynamic group membership. Evans and Bastian (1969) proposed that the spatial consideration of primary importance to

[12]Leatherwood, S. 1977. Some preliminary impressions on the numbers and social behavior of free swimming bottlenosed dolphin calves (*Tursiops truncatus*) in the northern Gulf of Mexico. *In* S. H. Ridgway and K. W. Benirschke (editors), Breeding dolphins, present status, suggestions for the future, p. 143-167. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PB-273 673.

[13]W. F. Perrin, fishery biologist, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92037, pers. commun. March 1980.

[14]Leatherwood, S., and M. F. Platter. 1975. Aerial assessment of bottlenosed dolphins off Alabama, Mississippi, and Louisiana. *In* D. K. Odell, D. B. Siniff, and G. H. Waring (editors), *Tursiops truncatus* Assessment Workshop, p. 49-86. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PD-291-161.

free-ranging bottlenose dolphins may be inter-individual distances and ease of access to the surface for breathing. The size of the herd home range of *Tursiops truncatus*, the frequently changing group compositions, and the number of bottlenose dolphins apparently residing in the study area suggest that the social organization is very complex.

Food Resources and Feeding Behavior

Striped mullet, *Mugil cephalus*, one of the four most common fish species in the Gulf of Mexico (Gunter 1941), is thought to be the mainstay of the diet of bottlenose dolphins (Gunter 1942; D. K. Caldwell and M. C. Caldwell 1972). Seasonal movements and ranges of tagged striped mullet have been determined in several areas of the gulf coast (Idyll and Sutton 1952; Broadhead and Mefford 1956; de Sylva et al. 1956; Ingle et al. 1962). Usually, the fish remained within 32 km of the capture location, but there is little documentation of daily movements. Local commercial fishermen reported that striped mullet spawn in the Gulf of Mexico in November and remain there until spring. Bottlenose dolphin movements from inshore to gulf waters in November thus appear to be similar to those of their primary prey.

Reports by Futch (1966) and local commercial fishermen indicated that the fish movements, and therefore bottlenose dolphin feeding activities, may also be influenced by the tides. Apparently striped mullet are often found in small groups on the shallow banks of bays and estuaries during the flood tide, and gather into larger schools in deeper water as the tide begins to ebb. Dolphin movements and feeding activities cannot be directly correlated with fish distributions in our study area, but such correlations have been reported for nearshore groups of bottlenose dolphins (Würsig and Würsig 1979) and humpback dolphins (Saayman and Tayler 1979).

We surveyed potential food resources of the bottlenose dolphin by interviewing and occasionally accompanying commercial fishermen in the study area. Although striped mullet were most commonly caught, significant numbers of pinfish, *Lagodon rhomboides*; sheepshead, *Archosargus probatocephalus*; and crevalle jack, *Caranx hippos*, were also taken in the same areas. According to fishermen, local dolphins prefer striped mullet, but when striped mullet are not plentiful will eat any available fish, including the hardhead catfish, *Arius felis*, which they swallow after detaching the head. Opportunistic feeding by bottlenose dolphins has also been noted in other areas (D. K. Caldwell and M. C. Caldwell 1972; Leatherwood 1975).

The use of radio tracking data to indicate feeding behavior has been proposed for the harbor porpoise, *Phocoena phocoena* (Gaskin et al. 1975), and small pelagic cetaceans (see reviews by Leatherwood and Evans 1979). Observations of apparent feeding by tagged and untagged bottlenose dolphins in our study area, however, suggested that respiratory intervals interpreted from breaks in transmitter signals were not a valid criterion to indicate foraging for this species. We believe that the long dives associated with foraging for pelagic species are not typical in the shallow habitat of our study area, and therefore transmitted dive times were relatively uniform. Dive intervals ranged from a few seconds to 4 min 25 s, but no relations between dive intervals and time of day were detectable. Lengths of hourly dives averaged 30-40 s, but varied with location and individual bottlenose dolphin.

Feeding strategies of bottlenose dolphins appear to vary with prey abundance and depth. Large compact groups of feeding bottlenose dolphins were seen in the Gulf of Mexico, although the dispersed foraging pattern reported for common dolphins (Evans 1971, 1974, 1975) and the spinner dolphin, *S. longirostris* (Norris and Dohl 1980b), was also evident. When foraging through shallow bays and grass flats, bottlenose dolphins typically formed slow-moving, dispersed groups. Humpback dolphins off South Africa (Saayman and Tayler 1973, 1979) and bottlenose dolphins off Argentina (Würsig and Würsig 1979) also forage close to shore in small groups. Dispersed feeding would be especially effective if the dolphins stayed in acoustic contact, then responded to certain signals by converging on a concentration of fish discovered by one or more individuals. This type of convergence on food sources has been proposed for dusky dolphins (Würsig and Würsig 1980). We did not observe dolphins rapidly converging on fish schools in shallow areas, but group members did occasionally move to an area where a single dolphin had paused to feed.

Shallow-water feeding was often characterized by a rapid erratic chase that ended in a sudden tight spin or pinwheel—the process lasting 1-5 s and covering 5-20 m. Fish sometimes leaped ahead of the approaching bottlenose dolphin and

were sometimes briefly observed in the bottlenose dolphin's mouth at the end of the chase. Similar behavior by feeding bottlenose dolphins has been described by Leatherwood (1975), Shane and Schmidly (footnote 5), and Shane (1980). The upside down feeding behavior reported for bottlenose dolphins (Leatherwood 1975) and humpback dolphins (Saayman and Tayler 1979) was occasionally observed. Obvious herding of fish as has been reported for several small cetaceans in nearshore areas (D. K. Caldwell and M. C. Caldwell 1972; Saayman et al. 1972; Tayler and Saayman 1972; Saayman et al. 1973; Leatherwood 1975; Saayman and Tayler 1979; Shane and Schmidly footnote 5) was not observed.

In the Gulf of Mexico (at depths of 3-6 m), rapid convergence by bottlenose dolphins within a radius of about 200 m was observed on several occasions. The bottlenose dolphins dove and remained submerged for 30-90 s in an area where no fish were obvious. Then a number of bottlenose dolphins surfaced almost simultaneously in a confined area amid large numbers of jumping striped mullet, some of which were captured in midair. Although cooperative feeding cannot be confirmed, at the very least the bottlenose dolphins were feeding on the same school of fish, and we suspect they may have herded the school at the surface in an organized way. This behavior differs somewhat from other accounts of cooperative feeding (see review by Norris and Dohl 1980a) because the fish school remained at the surface only briefly, after which the bottlenose dolphins milled in the area for 1-3 min before gradually dispersing into small groups. On one occasion, a sequence of rapid convergence on a concentrated fish school, brief intense feedings, and then dispersal into small groups was repeated three times within 45 min by 20-30 bottlenose dolphins.

Concentrated feeding at more productive areas may optimize food availability for flocking birds in the Mojave Desert (Cody 1971), and a similar strategy has been suggested for common dolphins (Evans 1971, 1974, 1975) and spinner dolphins (Norris and Dohl 1980a). These pelagic cetaceans may feed intensively, primarily after dusk and before dawn, in productive areas of the deep scattering layer before moving on. Theoretically, if the dolphins do not return to the same site for some time, the food source will replenish. In contrast, bottlenose dolphins in our study area may exert an almost constant pressure on available food resources. Inshore regions of the study area and the waters along the Gulf beaches were often traversed several times in a single day by different groups of foraging bottlenose dolphins. Evidence from captives and anecdotal accounts from commercial fishermen indicate that bottlenose dolphins also feed at night. Bottlenose dolphins may feed on different ecotypes in different geographic areas (Walker[15]), and presumably *T. truncatus* in coastal Florida have prey and feeding strategies different from bottlenose dolphins in pelagic habitats. Habitat differences are therefore important to any generalized concept of cetacean behavior and herd function. Because ecological variables influence social behavior and therefore the structure of small-cetacean herds (see reviews by Norris and Dohl 1980a; Wells et al. 1980), studies of adjacent inshore and offshore populations of bottlenose dolphins could do much to elucidate the influence of habitat on cetacean behavior.

Reproduction and Growth

Calves were defined as noticeably smaller bottlenose dolphins closely associating with a single larger animal and composed 8.2% of the bottlenose dolphins sighted. Extensive observations of tagged cow-calf pairs suggest that the above definition was generally applicable. Ten calves ($\bar{X}$ = 171 cm; SE = 9) represented 19% of all captures and recaptures. The relative number of calf sightings per month varied significantly ($P<0.0005$; chi-square contingency tables) from August 1975 to July 1976. It is not clear from the sighting data if the calves were produced during a bimodal breeding season with peaks in late spring and early fall, as suggested by Harrison and Ridgway (1971), or during a continuous breeding season with increases in activity during spring and fall. Many small cetaceans copulate throughout the year, and evidence for discrete breeding seasons is still contradictory (see review by Saayman and Tayler 1979).

Growth measurements were obtained from the repeated captures of calves and the recapture of a young individual originally captured in 1970 (Irvine and Wells 1972). Two calves were captured several times during the study; one grew from 172 to 183 cm in 13 mo, and the other from 189 to 198

[15]Walker, W. A. 1981. Geographical variation in morphology and biology of bottlenose dolphins (*Tursiops*) in the eastern North Pacific. Natl. Mar. Fish. Serv. Admin. Rep. LJ 81 03C. Unpubl. rep.

cm in 7 mo. A young bottlenose dolphin with a deformed jaw originally captured in 1970 grew from 185 to 219 cm in 5.3 yr.

ACKNOWLEDGMENTS

We gratefully acknowledge the many volunteers from New College (University of South Florida) and the University of Florida who donated a total of over 2,000 work hours during captures, radio tracks, surveys, and data analysis. We thank Grady Marlow and Mike Haslette and staff from the St. Petersburg Aquarium for the bottlenose dolphin collections through October 1975 and "Snake" Eubanks and Joe Mora for their fine work thereafter. We also thank John Morrill (New College, Environmental Studies Program) for providing office space, Mary Moore and Carol Blanton for furnishing dock space, Fred Worl for liquid nitrogen, and especially Fran and Jack Wells who provided floor space and much patience to the dolphin trackers who regularly invaded their home.

Field work was supported by Marine Mammal Commission Contracts MM4AC004 and MM5AC0018. William E. Evans of the Hubbs-Sea World Research Institute, David K. Caldwell of Biological Systems Inc., Clyde Jones and Howard Campbell of the Denver Wildlife Research Center, and Robert Hofman of the Marine Mammal Commission provided support and encouragement. We also thank Michael Bogan, Steven Leatherwood, Susan Shane, Peter Major, Dan Odell, Forrest G. Wood, and Bernd Würsig for their constructive review comments. Howard Kochman assisted with statistical computer analysis. Estella Duell and Luanne Whitehead typed early versions of the manuscript, and Esta Belcher and Russ Parks prepared the illustrations.

LITERATURE CITED

ASPER, E. D.
1975. Techniques of live capture of smaller cetacean. J. Fish. Res. Board Can. 32:1191-1196.

BARHAM, E. G., J. C. SWEENEY, S. LEATHERWOOD, R. K. BEGGS, AND C. L. BARHAM.
1980. Aerial census of the bottlenose dolphin, *Tursiops truncatus*, in a region of the Texas coast. Fish. Bull., U.S. 77:585-595.

BROADHEAD, G. C., AND H. P. MEFFORD.
1956. The migration and exploitation of the black mullet, *Mugil cephalus* L. in Florida, as determined from tagging during 1949-1953. Fla. State Board Conserv. Tech. Ser. 18, 32 p.

CALDWELL, D. K.
1955. Evidence of home range of an Atlantic bottlenose dolphin. J. Mammal. 36:304-305.

CALDWELL, D. K., AND M. C. CALDWELL.
1972. The world of the bottlenose dolphin. J. B. Lippincott Co., Phila., 157 p.

CALDWELL, D. K., AND F. B. GOLLEY.
1965. Marine mammals from the coast of Georgia to Cape Hatteras. J. Elisha Mitchell Sci. Soc. 81:24-32.

CALDWELL, M. C., AND D. K. CALDWELL.
1967. Intraspecific transfer of information via pulsed sound in captive odontocete cetaceans. *In* R. G. Busnel (editor), Les systèmes sonars animaux, biologie et bionique, Vol. 2, p. 897-936. Laboratoire de Physiologie Acoustique, Jouy-en-Josas, France.
1972. Behavior of marine mammals. *In* S. H. Ridgway (editor), Mammals of the sea: biology and medicine, p. 419-465. C. C. Thomas, Springfield, Ill.

CODY, M. L.
1971. Finch flocks in the Mohave Desert. Theoret. Pop. Biol. 2:142-158.

DE SYLVA, D. P., H. B. STEARNS, AND D. C. TABB.
1956. Populations of the black mullet (*Mugil cephalus* L.) in Florida. Fla. State Board Conserv. Tech. Ser. 19, 45 p.

EVANS, W. E.
1967. Vocalization among marine mammals. *In* W. N. Tavolga (editor), Marine bio-acoustics, Vol. 2, p. 159-186. Pergamon Press, N.Y.
1971. Orientation behavior of delphinids: Radio telemetric studies. Ann. N.Y. Acad. Sci. 188:142-160.
1974. Radio-telemetric studies of two species of small odontocete cetaceans. *In* W. E. Schevill (editor), The whale problem, p. 385-394. Harv. Univ. Press, Camb., Mass.
1975. Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* Linnaeus in the northeastern Pacific. Ph.D. Thesis, Univ. California, Los Ang., 145 p.

EVANS, W. E., AND J. BASTIAN.
1969. Marine mammal communication: social and ecological factors. *In* H. T. Anderson (editor), The biology of marine mammals, p. 425-475. Acad. Press, Lond.

EVANS, W. E., J. D. HALL, A. B. IRVINE, AND J. S. LEATHERWOOD.
1972. Methods for tagging small cetaceans. Fish. Bull., U.S. 70:61-65.

FUTCH, C. R.
1966. Lisa, the Florida black mullet. Fla. State Board Conserv. Mar. Lab., Salt Water Fish. Leafl. 6, 6 p.

GASKIN, D. E., G. J. D. SMITH, AND A. P. WATSON.
1975. Preliminary study of the movements of harbor porpoises (*Phocoena phocoena*) in the Bay of Fundy using radiotelemetry. Can. J. Zool. 53:1466-1471.

GUNTER, G.
1941. Relative numbers of shallow water fishes of the northern Gulf of Mexico, with some records of rare fishes from the Texas coast. Am. Midl. Nat. 26:194-200.
1942. Contributions to the natural history of the bottlenose dolphin, *Tursiops truncatus* (Montague), on the Texas coast, with particular reference to food habits. J. Mammal. 23:267-276.

HARRISON, R. J., AND S. H. RIDGWAY.
1971. Gonadal activity in some bottlenose dolphins (*Tursiops truncatus*). J. Zool. (Lond.) 165:355-366.

HOESE, H. D.
1971. Dolphin feeding out of water in a salt marsh. J. Mammal. 52:222-223.

IDYLL, C. P., AND J. W. SUTTON.
1952. Results of the first year's tagging of mullet, *Mugil cephalus* L., on the west coast of Florida. Trans. Am. Fish. Soc. 81:69-77.

INGLE, R. M., R. F. HUTTON, AND R. W. TOPP.
1962. Results of the tagging of salt water fishes in Florida. Fla. State Board Conserv. Mar. Lab. Tech. Ser. 38, 55 p.

IRVINE, B., AND R. S. WELLS.
1972. Results of attempts to tag Atlantic bottlenosed dolphins (*Tursiops truncatus*). Cetology 13:1-5.

KATONA, S., B. BAXTER, O. BRAZIER, S. KRAUS, J. PERKINS, AND H. WHITEHEAD.
1979. Identification of humpback whales by fluke photographs. *In* H. E. Winn and B. L. Olla (editors), Behavior of marine mammals, Vol. 3, p. 33-44. Plenum Press, N.Y.

LEATHERWOOD, S.
1975. Some observations of feeding behavior of bottlenosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops* cf. *T. gilli*) off southern California, Baja California, and Nayarit, Mexico. Mar. Fish. Rev. 37(9):10-16.
1979. Aerial survey of bottlenosed dolphin, *Tursiops truncatus*, and the West Indian manatee, *Trichechus manatus*, in the Indian and Banana Rivers, Florida. Fish. Bull., U.S. 77:47-59.

LEATHERWOOD, S., AND W. E. EVANS.
1979. Some recent uses and potentials of radiotelemetry in field studies of cetaceans. *In* W. E. Winn and B. L. Olla (editors), Behavior of marine mammals, Vol. 3, p. 1-31. Plenum Press, N.Y.

LEATHERWOOD, S., J. G. GILBERT, AND D. G. CHAPMAN.
1978. An evaluation of some techniques for aerial censuses of bottlenosed dolphins. J. Wildl. Manage. 42:239-250.

LEATHERWOOD, S., AND D. K. LJUNGBLAD.
1979. Nighttime swimming and diving behavior of a radio-tagged spotted dolphin, *Stenella attenuata*. Cetology 34, 6 p.

LEATHERWOOD, S., AND R. R. REEVES.
1978. Porpoises and dolphins. *In* D. Haley (editor), Marine mammals of eastern North Pacific and Arctic waters, p. 97-111. Pacific Search Press, Seattle.

MARTIN, H., W. E. EVANS, AND C. A. BOWERS.
1971. Methods for radio tracking marine mammals in the open sea. IEEE, Conf. Eng. Ocean Environ., p. 44-49.

MCBRIDE, A. F., AND H. KRITZLER.
1951. Observations on pregnancy, parturition, and post-natal behavior in the bottlenose dolphin. J. Mammal. 32:251-266.

MEAD, J. G.
1975. Preliminary report on the former net fisheries for *Tursiops truncatus* in the western north Atlantic. J. Fish. Res. Board Can. 32:1155-1162.

MIYAZAKI, N., AND M. NISHIWAKI.
1978. School structure of the striped dolphin off the Pacific coast of Japan.. Sci. Rep. Whales Res. Inst. 30:65-115.

NORRIS, K. S., AND T. P. DOHL.
1980a. The structure and functions of cetacean schools. *In* L. M. Herman (editor), Cetacean behavior: Mechanisms and functions, p. 211-261. Wiley, N.Y.
1980b. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fish. Bull., U.S. 77:821-849.

NORRIS, K. S., AND J. H. PRESCOTT.
1961. Observations on Pacific cetaceans of Californian and Mexican waters. Univ. Calif. Publ. Zool. 63:291-401.

NORRIS, K. S., AND K. W. PRYOR.
1970. A tagging method for small cetaceans. J. Mammal. 51:609-610.

OVERTON, W. S.
1972. Estimating the numbers of animals in wildlife populations. *In* R. H. Giles, Jr. (editor), Wildlife management techniques, 3d ed., p. 403-456. Wildl. Soc., Wash., D.C.

PAYNE, R.
1976. At home with right whales. Natl. Geogr. 149: 325-339.

PERRIN, W. F.
1975. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. J. Fish. Res. Board Can. 32:1059-1067.

PIKE, G. C.
1953. Colour pattern of humpback whales from the coast of British Columbia. J. Fish. Res. Board Can. 10:320-325.

PILLERI, G., AND J. KNUCKEY.
1968. The distribution, navigation and orientation by the sun of *Delphinus delphis* L. in the western Mediterranean. Experientia 24:394-396.

SAAYMAN, G. S., D. BOWER, AND C. K. TAYLER.
1972. Observations on inshore and pelagic dolphins on the south-eastern cape coast of South Africa. Koedoe 15:1-24.

SAAYMAN, G. S., AND C. K. TAYLER.
1973. Some behaviour patterns of the southern right whale *Eubalaena australis*. Z. Saugetierkunde 38:172-183.
1979. The socioecology of humpback dolphins (*Sousa* sp.). *In* H. E. Winn and B. L. Olla (editors), Behavior of marine mammals, vol. 3, p. 165-226. Plenum Press, N.Y.

SAAYMAN, G. S., C. K. TAYLER, AND D. BOWER.
1973. Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus* Ehrenberg). Behaviour 44:212-233.

SERGEANT, D. E., K. K. CALDWELL, AND M. C. CALDWELL.
1973. Age, growth, and maturity of bottlenosed dolphin (*Tursiops truncatus*) from northeast Florida. J. Fish. Res. Board Can. 30:1009-1011.

SHANE, S. H.
1980. Occurrence, movements, and distribution of bottlenose dolphin, *Tursiops truncatus*, in southern Texas. Fish. Bull., U.S. 78:593-601.

SOKAL, R. R., AND J. J. ROHLF.
1969. Biometry; the principles and practice of statistics in biological research. Freeman, San Franc., 776 p.

TAVOLGA, M. C.
1966. Behavior of the bottlenose dolphin (*Tursiops truncatus*): social interactions in a captive colony. *In* K. S. Norris (editor), Whales, dolphins, and porpoises, p. 718-730. Univ. Calif. Press, Berkeley.

TAYLER, C. K., AND G. S. SAAYMAN.
1972. The social organization and behavior of dolphins (*Tursiops truncatus*) and baboons (*Papio ursinus*): some comparisons and assessments. Ann. Cape Prov. Mus. (Nat. Hist.) 9:11-49.

TRUE, F. W.
1885. The bottle-nose dolphin, *Tursiops tursio*, as seen at Cape May, New Jersey. Science (Wash., D.C.) 5:338-339.

WELLS, R. S.
1978. Home range characteristics and group composition of Atlantic bottlenosed dolphins, *Tursiops truncatus*, on the west coast of Florida. M.S. Thesis, Univ. Florida, Gainesville, 91 p.

WELLS, R. S., A. B. IRVINE, AND M. D. SCOTT.
1980. The social ecology of inshore odontocetes. *In* L. M. Herman (editor), Cetacean behavior, p. 263-317. Wiley-Intersci., N.Y.

WILSON, E. O.
1975. Sociobiology: the new synthesis. Harv. Univ. Press, Camb., Mass., 697 p.

WÜRSIG, B.
1978. Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine bay. Biol. Bull. (Woods Hole) 154:348-359.
In press. Radio tracking dusky porpoises in the South Atlantic. *In* Mammals in the seas, U.N., FAO Fish. Ser. 5.

WÜRSIG, B., AND M. WÜRSIG.
1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science (Wash., D.C.) 198:755-756.
1979. Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. Fish. Bull., U.S. 77:399-412.
1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. Fish. Bull., U.S. 77:871-890.

MAXIMUM YIELD ESTIMATES FOR THE PACIFIC THREAD HERRING, *OPISTHONEMA* SPP., FISHERY IN COSTA RICA

DAVID K. STEVENSON[1] AND FRANCISCO CARRANZA[2]

ABSTRACT

Linear and exponential surplus production models were applied to annual 1969-79 catch per unit effort and effort data obtained from the Costa Rican Pacific thread herring fishery. Effort was estimated as the number of calendar days at sea and standardized to account for presumed increases in fishing power and "real" fishing time (time spent searching for fish) after 1973. Independent regression analyses were performed using standardized and unstandardized effort estimates. In addition, values of the independent variable were estimated both as simple annual effort and as a moving 2-year average of effort. All regressions were statistically significant, but the best fit was obtained with standardized average effort and the exponential model. The "best" estimates of maximum equilibrium yield and effort (Y_s = 6,430 t; f_s = 1,036 days or 1,096 standard days) indicated that the resource was overexploited in 1974-75, 6 years after fishing began. In 1976-77 catch remained at approximately Y_s levels while effort remained above f_s. Catch and observed effort declined dramatically during 1978-79 although standardized effort remained slightly above 1,100 standard days. Future management of the resource may require limited catch and/or effort. The validity of the model is discussed primarily in terms of the nonindependence of the X and Y variables.

Thread herring (genus *Opisthonema*) are schooling pelagic clupeids which inhabit tropical and subtropical coastal waters of the western Atlantic and eastern Pacific Oceans. According to Berry and Barrett (1963), three Pacific species (*Opisthonema libertate*, *O. bulleri*, and *O. medirastre*) are found in continental waters between northern Mexico and Peru while a fourth species (*O. berlangai*) is limited to the Galapagos Islands. These authors differentiated individual species on the basis of the number of gill rakers, a meristic character which was found to be positively related to standard length. The most abundant Atlantic species (*O. oglinum*) is distributed from southern Brazil to the Gulf of Maine.

Thread herring school in nearshore waters (Klima 1971; Magnusson 1971) and are planktivorous feeders. Fuss et al. (1969) observed copepods and larval pelecypods, gastropods, and barnacles in the stomachs of Atlantic thread herring. Peterson (1956) reported mostly phytoplankton from Pacific thread herring stomachs collected in Costa Rica. The presence of fine sediments in the stomachs of Atlantic thread herring indicated that these fish may spend some time feeding on the bottom.

Atlantic thread herring spawn during April-August in the eastern Gulf of Mexico. Fuss et al. (1969) reported a maximum mean gonad index in June, and Houde (1976) collected eggs when surface seawater temperature ranged from 22.5° to 30° C. Most eggs and larvae were collected within 50 km of the coast. Based on the histological examination of reproductive tissue, Paez Barrera[3] reported peak spawning for *O. libertate* in Mexico during June and July at water temperatures of 25°-29° C. Peterson (1956) collected small individuals (<60 mm SL, standard length) in the Gulf of Nicoya, Costa Rica, during all months of the years 1952-54. His observations indicated that spawning may have been continuous. Furthermore, nearly all collections of adults included some individuals which were sexually mature. Continuous recruitment on the Pacific coast of Costa Rica was also implied by the presence of a predominant size group at 18-20 cm SL in most

[1]Department of Zoology, University of Maine, Orono, ME 04469 or Maine Department of Marine Resources, West Boothbay Harbor, ME 04575.

[2]Departamento de Estudios Biológicos de Fauna Marina y Continental, Ministerio de Agricultura y Ganadería, San Jose, Costa Rica.

[3]Paez Barrera, F. 1976. Desarrollo gonadal, madurez, desove y fecundidad de sardina crinuda, *Opisthonema libertate* (Gunther) de la zona de Mazatlán, basados en el analisis histológico de la gónada. Mem. del Simp. sobre Recursos Masivos de México, Ensenada, B.C., 28-30 de Septiembre de 1976, p. 207-255.

Manuscript accepted May 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

monthly length-frequency distributions compiled from commercial landings by the Costa Rican Ministry of Agriculture during 1975-77.

Attempts to determine the age and growth of *Opisthonema* spp. based on apparent scale annuli and length-frequency analyses have not produced very satisfactory results, presumably since growth rates and recruitment are more or less continuous throughout the year. Reintjes[4] reported that few Atlantic thread herring live beyond age 4, and Sokolov and Wong[5] speculated that there were three adult year classes of *O. libertate* within the harvestable size range (5-26 cm SL) in the Gulf of California. Paez Barrera (footnote 3) reported a minimum length at maturity of 13-14 cm SL for *O. libertate* in Mexico. Houde (1976) reported that age 1 Atlantic thread herring measured approximately 13 cm SL. Length-frequency distributions for *Opisthonema* spp. sampled from commercial landings in Costa Rica were commonly characterized by a single predominant size group at 18-20 cm SL, but occasionally included a second group at 12-16 cm SL.

Although he presented no information for *Opisthonema*, Beverton (1963) indicated that most clupeid and engraulid species are short lived (5 yr or less) and are generally characterized by high growth and mortality rates. Furthermore, these fish mature at relatively early ages (age at maturity/maximum age = 0.30-0.37) and grow very little after maturing (length at maturity/maximum length = 0.65-0.80) compared with other taxonomic groups. High mortality rates (Z = 0.5-3.0) can be largely attributed to the active predation on these fish by man, birds, and other fish. Highly variable recruitment has contributed to the decline of many stocks of small pelagic fishes for which recruitment appears to be independent of spawning stock size over a wide range of stock sizes (Murphy 1977).

The most important thread herring fisheries are conducted on the Pacific coast of Central and South America. Most of the 1972-77 catch of Pacific thread herring was landed in Ecuador (Table 1) where landings increased by 700% during this 6-yr period. Panama and Mexico accounted for <10% of the total reported landings in 1976 and 1977. Thread herring are harvested with the Pacific sardine, *Sardinops sagax*, in Mexico and are utilized both for human consumption and for fish meal. Thread herring are harvested incidentally to the anchoveta, *Centengraulis mysticetus*, in the Gulf of Panama and reduced to meal. Thread herring fisheries do not presently exist in any of the remaining Central American countries except Costa Rica where, by law, the total production is canned for human consumption.

TABLE 1.—Annual 1972-77 landings (thousand metric tons) of Pacific thread herring in Ecuador, Panama, and Mexico. Sources: FAO Yearbook of Fishery Statistics (1979) and Instituto Nacional de Pesca, Mexico.

Country	1972	1973	1974	1975	1976	1977
Ecuador	552	950	1,100	1,750	2,250	3,830
Panama	143	205	367	201	166	234
Mexico	18	36	22	32	35	65
Total	713	1,191	1,489	1,983	2,451	4,129

Thread herring have been harvested on the Pacific coast of Costa Rica since 1968. The fleet expanded steadily from a single vessel in 1968-69 to nine vessels in 1975. At present the fleet consists of 10 vessels, although only half the fleet may be active at any one time. Most of the fish landed during 1968-73 were harvested in the outer Gulf of Nicoya (Figure 1) and from coastal waters immediately to the south. Purse seiners and trawlers have been prohibited from fishing in the interior of the Gulf of Nicoya since 1975. The fishery expanded as far south as Golfo Dulce near the Panamanian border in 1972. Total catch reached a maximum of 7,500 t in 1975 and declined to about 5,000 t in 1978 and 1979, while total catch per day at sea peaked in 1971 (Figure 2). Catch in the Gulf of Nicoya peaked at 5,000 t in 1972 (Figure 3) and at 2,800 t in Golfo Dulce during 1975 (Figure 4).

The thread herring resource supports a small but important industry in Costa Rica. Landings in 1978 accounted for 36% of all fish and shellfish landed by the domestic fleet and $76,635 in ex-vessel revenue. Most of the herring canned in Costa Rica is sold domestically. A small quantity (9% in 1977) is exported to other Central American countries. There are three canning plants in the country, two in Puntarenas and one in Golfito. Eight of the existing 10 vessels are based in Puntarenas.

The objective of this study was to determine, from historical catch and effort data compiled by

[4]Reintjes, J. W. 1979. A review of the clupeoid and carangid fishery resources in the western central Atlantic. Interregional Project for the Development of Fisheries in the Western Central Atlantic (WECAF), 49 p.

[5]Sokolov, V. A., and M. I. Wong. 1973. Informe científico de las investigaciones sobre los peces pelágicos del Golfo de California (sardina crinuda y anchoveta) en 1971. Inst. Nac. Pesca, Inf. Cién. 2, 41 p.

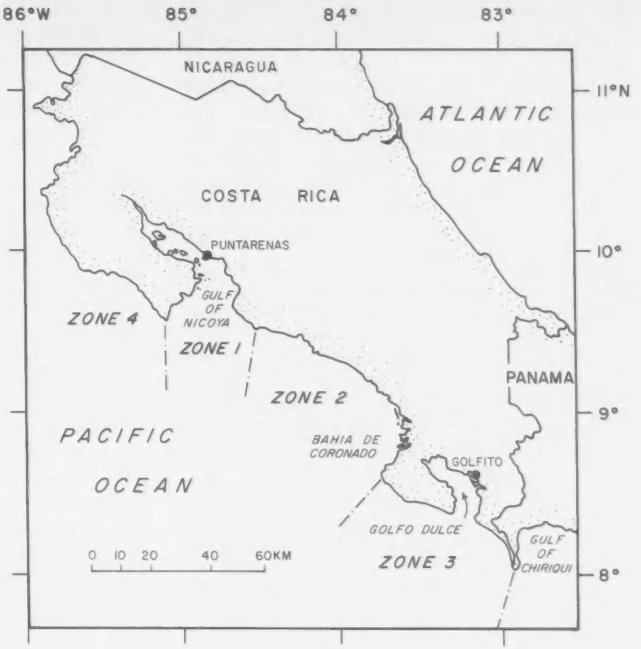

FIGURE 1.—Map of Costa Rica showing four thread herring fishing zones and two principal ports on the Pacific coast.

the Costa Rican Ministry of Agriculture, the maximum equilibrium yield which this resource will support and the amount of fishing effort required to achieve complete utilization. The methodology and the simplifying assumptions used in this study were necessary given the scarcity of biological information, the absence of species-specific catch data, and the nature of available effort statistics, and illustrate some of the problems which impede stock assessments in developing countries.

DEFINITION OF THE UNIT STOCK

Three species of *Opisthonema* are harvested on the Pacific coast of Costa Rica. Species identifica-

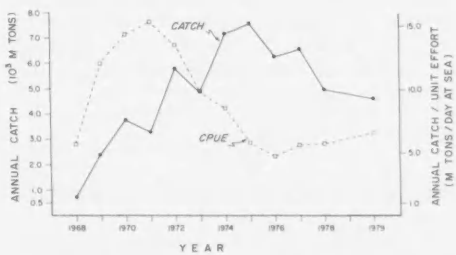

FIGURE 2.—Annual 1968-79 catch and catch per unit effort for three species of thread herring captured on the Pacific coast of Costa Rica (all zones). Catch and effort data were compiled from sales receipts.

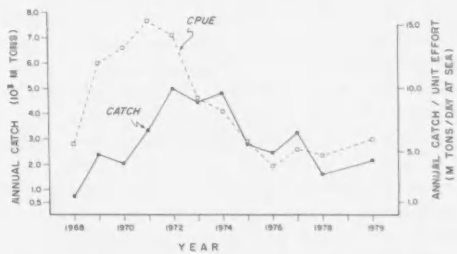

FIGURE 3.—Annual 1968-79 catch and catch per unit effort data for three species of thread herring captured in the Gulf of Nicoya, Costa Rica (zone 1). Catch and effort data were compiled from captain's reports and verified from sales receipts.

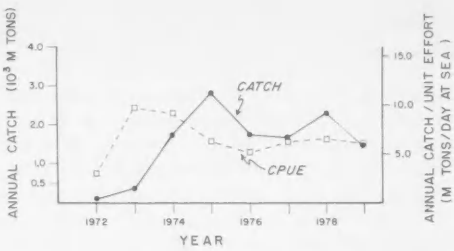

FIGURE 4.—Annual 1972-79 catch and catch per unit effort data for three species of thread herring captured in the Golfo Dulce area of Costa Rica (zone 3). Catch and effort were compiled from captain's reports and verified from sales receipts.

tion is based on the relation between the number of gill rakers and standard length (Berry and Barrett 1963). Over 3,000 specimens of thread herring collected from commercial catches by the Costa Rican Ministry of Agriculture during the period April 1975 to December 1977 were separated into two groups based on external coloration and morphological features. One group ("blue sardines") consisted of fish which more easily lost their scales and which were characterized by a blue dorsal coloration and more shallow, elongated bodies. These fish were predominantly *O. bulleri*. The second group ("green sardines") consisted primarily of *O. medirastre* and *O. libertate*. Fish in this group retained their scales, had deeper bodies, and a greener dorsal coloration. The second group was more abundant than the first, accounting for more than 90% of the fish sampled from commercial landings except during February-July 1977 when blue sardines made up 25-63% of the samples. Since the sampling procedures used were not strictly random and exact species identifications were not attempted, it can only be concluded that *O. medirastre* and *O. libertate* appeared to be the predominant species in the catch during most of the sampling period.

In the absence of species-specific catch and effort information all three species were, for the purposes of analysis, assumed to compose a single unit stock confined to Costa Rican coastal waters. The degree to which the different species shared common growth or natural mortality rates was not known, nor was it certain whether they school together and were thus exploited with the same intensity in the same areas. Although commercial fishermen in Costa Rica have observed that *O. libertate* and *O. medirastre* intermingle in the same schools, *O. bulleri* are rarely captured together with the other two species and apparently do not school with them. Berry and Barrett (1963) reported that the size ranges of all three coastal Pacific species collected in Central and South America were nearly equal, an observation that was generally confirmed in samples taken from commercial catches in Costa Rica and which indicated that all three species were equally susceptible to capture over the same size range. All three species harvested in Costa Rica during 1975-77 reached a maximum size of about 24 cm SL.

The assumption of a single geographic stock in Costa Rican waters was largely an arbitrary one since there was no information available concerning the migratory behavior of the Pacific species. Klima (1971) reported that Atlantic thread herring, *O. oglinum*, in the northeastern Gulf of Mexico seldom are found in depths >100 m and are most common in depths <40 m. Similar observations have been reported for Pacific thread herring in Central America (Magnusson 1971). Kinnear and Fuss (1971) reported seasonal north-south migrations of *O. oglinum* on the west coast of Florida in response to changes in surface water temperatures. A southerly fall migration of 6-7 mi/d has been observed for *O. oglinum* between North Carolina and Florida (Pristas and Cheek 1973). Since seawater temperatures along the Pacific coast of Central America presumably are more constant, such directed migration may not occur.

Despite the fact that the three coastal Pacific species of *Opisthonema* are distributed continuously from the Gulf of California to Peru (Berry and Barrett 1963), there is some justification for treating the Costa Rican thread herring resource as a single geographic unit stock since there are no fisheries for thread herring in any of the other Central American countries except Panama. In Panama, *Opisthonema* spp. are harvested only in the Gulf of Panama and not in the intervening coastal waters of western Panama between the Gulf and the Costa Rican border.

METHODS

Estimation of Catch and Effort Statistics

Total annual catch and effort data were compiled from sales receipts obtained from the canning companies in Puntarenas and Golfito (Table 2). Catch data were reliable since the entire catch in Costa Rican waters was harvested by Costa

TABLE 2.—Annual 1968-79 catch, effort, catch per unit effort, and average effort statistics for three species of thread herring captured on the Pacific coast of Costa Rica. Catch and effort data were compiled from sales receipts. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Year	C_t Catch (t)	f_t Effort (d at sea)	$\bar{f}$ Average effort $=\frac{1}{2}(f_t+f_{t-1})$ (d at sea)	C_t/f_t (t/d)
1968	726	130	65	5.59
1969	2,400	200	165	12.00
1970	3,765	264	232	14.26
1971	3,323	217	240	15.31
1972	5,822	431	324	13.51
1973	4,886	501	466	9.75
1974	7,193	844	672	8.52
1975	7,592	1,304	1,074	5.82
1976	6,330	1,350	1,327	4.69
1977	6,619	1,176	1,263	5.63
1978	5,034	884	1,030	5.70
1979	4,654	753	818	6.18

Rican vessels and sold for canning in these two ports. Effort was estimated from sales receipts as the number of calendar days at sea and recorded as the difference between the dates of departure and arrival in port. One day at sea was considered to include only 12 daylight hours since no fishing was conducted at night. Effort measurements included any daylight time spent in transit to and from port, time actually spent setting and retrieving the net, time spent searching for schools of fish, and any time lost for vessel repairs or other activities unrelated to the capture of fish.

Some information on the division of total effort was available from Ministry of Agriculture biologists who observed vessel activities during five fishing trips in the Gulf of Nicoya during August and September 1980 (Table 3). During a total of 95 h absent from port, 60 h (63%) were spent searching for fish, 23 h in setting and retrieving the net, and 12 h were lost in transit and other activities unrelated to fishing. An average of 8.6 h were spent working per calendar day. The fourth trip was the most productive trip in terms of catch per day, catch per hour search, and catch per total hours, but the first and second trips were the most productive in terms of catch per hour fishing. These observations tended to confirm the assumption that search time was the most significant component of total effort and indicated that catch per day, the index of CPUE (catch per unit effort) used in this assessment, compared more closely to catch per hour search than to catch per hour fishing with the net. Although these observations were recorded for a very short period of time and did not represent average fishing conditions for the entire fishery during that time, they do give an idea of how time at sea was apportioned for vessels fishing close to Puntarenas during trips of 2-3 d duration in 1980 when catches were poor.

The original 1974-79 effort data (Table 2) were adjusted to account for a presumed increase in the proportion of a 12-h day spent searching for fish as stock abundance declined and an improved capture efficiency associated with the construction of larger, more powerful vessels using larger nets. In the absence of reliable information on the decline in resource availability or increased vessel fishing power, the standardization procedures which were applied were very approximate, but served in some degree to counteract the probable underestimation of real fishing effort during the later years of the fishery as measured simply by the number of days at sea. The year 1974 was selected as the critical year to initiate effort standardization since it was in 1974 that the fleet, in response to declining yields in the Gulf of Nicoya, expanded operations in earnest to more distant fishing grounds (Table 4) and increased in size from five active vessels to seven. The fleet continued to exploit more distant fishing grounds during subsequent years and expanded to nine active vessels in 1975-77. Most of the larger vessels were first

TABLE 3.—Detailed catch and effort information recorded by observers aboard thread herring vessels fishing in the Gulf of Nicoya, Costa Rica, during August and September 1980. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Trip	Days[1]	Hours	H/d	Sets	Catch[2] (t)	Search time (%)	Catch per unit effort t/d	t/h search	t/fishing h	t/total h
1	2	22.7	11.4	2	32.0	55	16.0	2.2	4.7	1.4
2	2	16.5	8.2	5	19.0	47	9.5	2.4	5.4	1.2
3	3	27.7	9.2	6	12.0	76	4.0	.6	2.9	.4
4	[3]1	11.9	11.9	4	22.5	39	22.5	4.9	4.0	1.9
5	3	15.9	[4]5.3	5	2.5	74	.8	.2	.8	.2
All	11	94.7	8.6	24	88.0	63	8.0	1.5	3.8	.9

[1]Calendar days absent from port.
[2]Estimated by captain.
[3]Two days were spent tuna fishing.
[4]Trip terminated early morning of day 3 due to equipment failure.

TABLE 4.—Distribution of reported 1968-79 fishing effort for thread herring among the three principal fishing zones on the Pacific coast of Costa Rica and percent of total effort expended in zones two and three. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Year	Effort (d at sea) Zone 1	Zone 2	Zone 3	% total effort in zones 2-3[1]
1968	130	0	0	0.0
1969	200	0	0	0.0
1970	154	110	0	41.7
1971	217	0	0	0.0
1972	351	45	35	18.6
1973	458	8	35	8.6
1974	584	64	187	29.7
1975	490	344	451	61.0
1976	628	359	334	51.3
1977	622	251	270	44.3
1978	339	188	349	60.7
1979	371	125	255	50.5

[1]Total effort includes a small amount of fishing in zone 4 which is not shown in this table.

registered in 1973 or later (Table 5). At least one of the newer vessels was equipped with directional sonar equipment, an addition which greatly aids in the location of schools.

TABLE 5.—Characteristics of purse seine vessels and gear which constituted the Costa Rican thread herring fleet in 1979. Vessels are ranked according to net tonnage and fall roughly into two groups according to size, horsepower, and the size of the net used by each vessel. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Vessel	Year registered	Net tonnage (t)	Length (m)	Capacity (t)	Horsepower	Net size (m)
			Group 1			
1	1975	20	13.7	—	150	—
2	1971	30	15.2	27	180	324 × 32
3	1971	33	17.1	33	125	324 × 32
4	1973	35	17.7	30	180	324 × 32
5	1971	40	15.2	38	40	324 × 32
6[1]	1973	40	18.9	45	228	360 × 45
			Group 2			
7	1973	42	24.4	60	500	450 × 36
8	1973	51	24.4	70	420	450 × 36
9	1973	56	26.5	120	360	504 × 36
10	1977	70	22.9	70	240	—
11	1975	75	22.9	60	330	486 × 54

[1]This vessel was lost at sea in October 1979.

Original 1974-79 effort data were adjusted (Table 6) to account for increased search time by increasing observed effort in five 5% annual increments beginning in 1975 and by a constant 25% annual increment to account for increased fishing power beginning in 1974. The first adjustment was based on the presumption that no more than 5 h in an average 12-h day (or 50% of the total fishing time after deducting 2 h for travel to and from port) were spent searching for fish in the early years of the fishery when fishing was concentrated primarily in the Gulf of Nicoya (Table 4), whereas 9 out of 12 h (75%) may have been spent searching for fish in 1979, assuming that the fish were less abundant and that vessels which travelled longer distances to and from fishing grounds in zones two and three devoted most of their daylight transit time to searching. This last assumption has in fact been confirmed by vessel captains. Observations made aboard vessels fishing near Puntarenas in 1980 during only 11 d (Table 3) showed that 63% of the daylight hours were devoted to searching. Since catch data originally collected for individual vessels and trips were no longer available when this assessment was conducted, the relative fishing power of individual vessels and the factors affecting vessel performance could not be determined.

Yield Analyses

Maximum equilibrium yield (Y_s) and its corresponding effort (f_s) were estimated by applying the linear and exponential forms of the surplus production model to annual catch and effort data compiled during 1969-79. These data were collected beginning in 1968 when fishing began and represented fishing activity during an initial period of high CPUE and low effort, an intermediate period when larger vessels were built and

TABLE 6.—Annual 1974-79 catch, adjusted effort and adjusted catch per unit effort (CPUE) statistics for three species of thread herring captured on the Pacific coast of Costa Rica. Original effort data were adjusted to account for a presumed 25% annual increase in vessel fishing power beginning in 1974 and an additional 5% annual increment to account for a presumed increase in search time per day at sea beginning in 1975.

Year	Catch C_t (t)	Original effort f_t (d at sea)	Correction factor x_t	Adjusted effort xf_t (standard d)	Adjusted CPUE C_t/xf_t (t/standard d)	Average effort $\frac{1}{2}(xf_t + xf_{t-1})$ (standard d)
1974	7,193	844	1.25	[1]1,055	6.82	778
1975	7,592	1,304	1.30	1,695	4.48	1,375
1976	6,330	1,350	1.35	1,822	3.47	1,758
1977	6,619	1,176	1.40	1,646	4.02	1,734
1978	5,034	554	1.45	1,282	3.93	1,464
1979	4,654	753	1.50	1,130	4.12	1,206

[1]xf_t in 1973 was 1.0(501 d) = 501 d.

the fleet expanded to new fishing grounds in response to declining CPUE and a later period characterized by diminished total production and severely reduced CPUE throughout the entire geographic range of the fishery. Estimates of maximum equilibrium yield and the amount of fishing effort required to produce that yield could serve as "starting points" for management strategies intended to conserve the Costa Rican thread herring resource and achieve maximum social and economic benefits from the fishery.

The linear surplus production model was first outlined by Graham (1935) and further developed by Schaefer (1954). These authors postulated that under equilibrium conditions the instantaneous rate of surplus production from a given population at any time (t) is directly proportional to the biomass (B_t) of the population at that time and to the difference between the theoretical maximum biomass (B_∞) and B_t and inversely proportional to B_∞, i.e.

$$\frac{dB}{dt} = \frac{kB_t(B_\infty - B_t)}{B_\infty} \tag{1}$$

where k = the instantaneous rate of increase in stock size at densities approaching zero.

Moreover, when the biomass which exceeds an equilibrium level (B_E) is being removed at the same rate as it is produced, the surplus production (dB/dt) is converted into an annual equilibrium yield (Y_E) according to the following expression:

$$\frac{dB}{dt} = Y_E = F_E B_E \tag{2}$$

where F_E = rate of fishing which maintains the population at B_E.

If we assume that the rate of fishing (or instantaneous rate of fishing mortality) at equilibrium is proportional to the fishing intensity (or effort) then

$$F_E = qf_E \tag{3}$$

where f_E = fishing effort under equilibrium conditions

q = the coefficient of "catchability," i.e., the vulnerability of the population to fishing.

From Equations (1) and (2), at equilibrium

$$\frac{dB}{dt} = Y_E = F_E B_E = \frac{kB_E(B_\infty - B_E)}{B_\infty}. \tag{4}$$

Substituting Y_E/F_E for B_E in Equation (4)

$$Y_E B_E = F_E B_\infty - \frac{B_\infty}{k} F_E{}^2 \tag{5}$$

and from Equation (3)

$$Y_E = qB_\infty f_E - \frac{q^2 B_\infty}{k} f_E{}^2 \tag{6}$$

which defines a parabola in which Y_E is a function of f_E.

Dividing both sides of Equation (6) by f_E yields a linear relationship $Y_E/f_E = a + bf_E$ where the intercept $a = qB_\infty$ and the slope $b = q^2B_\infty/k$. The effort f_s which corresponds to the maximum equilibrium catch Y_s is determined from the relationship

$$\frac{dY_E}{df_E} = a - 2bf_E = 0. \tag{7}$$

Therefore

$$f_E - f_s = \frac{a}{2b}. \tag{8}$$

Substituting Equation (8) in Equation (6), the maximum equilibrium yield Y_s determined from the regression function is

$$Y_E = Y_s = \frac{a^2}{4b}. \tag{9}$$

Thus, when Equation (3) is valid, estimates of maximum equilibrium yield and associated effort

can be obtained from CPUE and effort data compiled from a unit stock fishery under equilibrium conditions even when the catchability coefficient (q) is unknown.

Since catch and CPUE will usually be related to effort within a single year and during several preceding years, Gulland (1969) has argued that the abundance of a particular year class which has been in the fishery for x years would be influenced by the fishing mortalities during those x years and proposed that the total CPUE for all ages during any given year would be related to some weighted mean of fishing effort in those x years. According to Gulland (1969), if this mean is taken over a period of time equal to the mean duration of life in the exploited phase, then the relation between CPUE and this mean effort $\bar{f}$ will approximate that between CPUE and effort in the steady state.

An exponential form of the surplus production model was developed by Fox (1970) to express the nonlinear relationship between CPUE and effort statistics. The exponential surplus production model was based on the assumption that the rate of population increase was best described by the Gompertz growth function rather than the logistic growth function assumed by the linear form of the model. For the exponential model, under equilibrium conditions

$$\frac{dB}{dt} = kB_E(\log_e B_\infty - \log_e B_E) \qquad (10)$$

and the annual equilibrium yield (Y_E) is therefore

$$\frac{dB}{dt} = Y_E = kB_E(\log_e B_\infty - \log_e B_E). \qquad (11)$$

Since CPUE ($Y/f = U$) is defined to be proportional to population biomass

$$B_E = \frac{1}{q}\left(\frac{Y_E}{f_E}\right) = \frac{U_E}{q}, \qquad (12)$$

Equation (11) can be rewritten as

$$\frac{dB}{dt} = Y_E = \frac{U_E}{q}k\left(\log_e \frac{U_\infty}{q} - \log_e \frac{U_E}{q}\right). \qquad (13)$$

Collecting terms and dividing through by U_E ($= Y_E/f_E$)

$$f_E = \frac{k}{q}(\log_e U_\infty - \log_e U_E) \qquad (14)$$

or

$$\log_e U_E = \log_e U_\infty - \left(\frac{q}{k}\right)f_E \qquad (15)$$

which is equivalent to

$$U_E = U_\infty e^{-bf_E}. \qquad (16)$$

Multiplying Equation (16) by the fishing effort at equilibrium (f_E)

$$Y_E = f_E U_\infty e^{-bf_E}. \qquad (17)$$

Therefore, the effort (f_s) which produces maximum equilibrium yield (Y_s) is determined from the relationship

$$\frac{dY_E}{df_E} = -bf_E U_\infty e^{-bf_E} + U_\infty e^{-bf_E} = 0 \qquad (18)$$

and

$$f_s = \frac{1}{b}. \qquad (19)$$

Since $bf_s = 1$, CPUE at f_s (U_s) is

$$U_s = U_\infty e^{-bf_s} = \frac{U_\infty}{e} \qquad (20)$$

and the maximum equilibrium yield (Y_s) is given by

$$Y_s = f_s U_s = \frac{U_\infty}{be}. \qquad (21)$$

Y_s and f_s were estimated from linear and exponential regressions of CPUE vs. effort when the effort corresponding to a given year's catch was set equal to effort applied during the same year (f_t), or an average of the effort applied buring the same year and the previous year ($\bar{f}$). For the purposes of calculating average effort, it was assumed that thread herring exploited in Costa Rican waters were recruited to the fishery at age 1 and remained in the exploitable size range for 3 yr. Effort was therefore averaged for a 2-yr period according to the procedure described by Gulland (1969) on the presumption that the mean duration of life in the exploitable size range was 2 yr. This assumption was generally supported by age and growth observations for species of this genus (Houde 1976; Sokolov and Wong footnote 5; Paez Barrera footnote 3; Reintjes footnote 4) but needs to be confirmed by specific growth studies.

A total of eight pairs of Y_s and f_s estimates were obtained from both the original and standardized data sets (Table 7). Analysis of the variance due to random error after regression was evaluated by calculating F-statistics. All regressions were performed for 1969-79 data since the 1968 catch was extremely low relative to the amount of effort expended (Table 3), suggesting that the single vessel which was in operation that year was not performing to its full capacity. For each model, predicted yield values for f_E = average observed effort and f_E = average standardized effort were plotted and compared with actual annual 1969-79 yields. Values of equilibrium yield (Y_E) predicted by each model for given values of equilibrium effort (f_E) were calculated according to

$$Y_E = af_E - bf_E{}^2 \qquad (22)$$

for the linear model, and

$$Y_E = af_E e^{-bf_E} \qquad (23)$$

for the exponential model.

RESULTS AND DISCUSSION

The results (Table 7) indicated a range of Y_s and f_s estimates depending on the model, the form of the independent variable (f_t or $\bar{f}$), and whether or not effort was standardized. For all cases, Y_s ranged from 6,290 to 7,890 t. A wider range of Y_s estimates was predicted by the linear model (6,700-7,890 t) as compared with the exponential model (6,290-6,730 t). Observed f_s estimates ranged from 888 to 1,067 d and standardized f_s estimates ranged from 1,041 to 1,117 standard days. Given the range of options which were tested, these ranges were not extreme. All regressions were statistically significant at >99% confidence levels.

Based on the "goodness of fit" as evaluated by the F-statistic, $\bar{f}$ produced a better fit than f_t in all cases, as did the exponential model as opposed to the linear model and the standardization of effort. The improved fit of the exponential model to CPUE vs. average observed and average standardized effort graphically was quite obvious (Figures 5, 6). Examining the independent effects on maximum equilibrium yield estimates produced by the standardization of effort data and the use of two different models, it was apparent that within each model standardization of the 1974-79 data increased Y_s, especially in the case of the linear model whereas use of the exponential model decreased Y_s estimates for both the standardized and observed data, but more significantly with the standardized data. Furthermore, the choice of f_t or $\bar{f}$ as the independent variable had very little effect on the magnitude of these changes. Looking at the

TABLE 7.—Summary of maximum equilibrium yield (Y_s), the amount of fishing effort which produces maximum equilibrium yield (f_s), and Y_s/f_s estimates for the Costa Rican thread herring fishery as derived from linear and exponential surplus production models applied to 1969-79 catch per unit effort and effort data. Linear and exponential regressions were repeated using effort data collected during the same year (f_t) and average effort over a 2-yr period ($\bar{f}$) as well as observed and adjusted effort estimates (see Tables 2, 6). Analyses of variance (F-tests) indicated that all regressions were statistically significant at 99% confidence levels.

Model	Effort	Y-intercept a	Slope × 10^3 b	Y_s[1] (t)	f_s (d at sea)	Y_s/f_s (t/d)	F-statistic
Linear	f_t observed	15.21	−8.317	6,950	914	7.60	41.4
	$\bar{f}$ observed	15.09	−8.494	6,700	888	7.54	61.5
	f_t adjusted	14.81	−6.952	7,890	[2]1,065	[2]7.41	58.4
	$\bar{f}$ adjusted	14.51	−6.969	7,550	[2]1,041	[2]7.25	64.8
Exponential	f_t observed	16.61	− .937	6,520	1,067	6.11	54.2
	$\bar{f}$ observed	16.50	− .965	6,290	1,036	6.07	114.7
	f_t adjusted	16.39	− .895	6,730	[2]1,117	[2]6.02	79.2
	$\bar{f}$ adjusted	15.96	− .912	6,430	[2]1,096	[2]5.87	138.8

[1]Rounded off to the nearest 10 t.
[2]Effort expressed in standard days at sea.

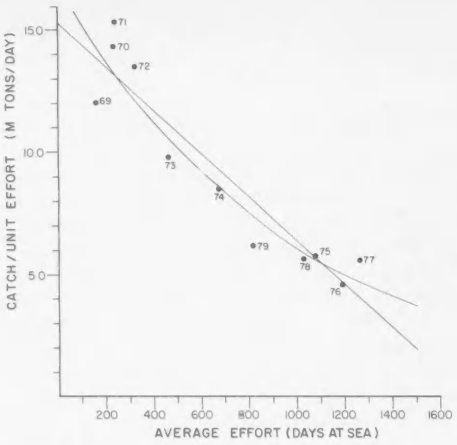

FIGURE 5.—Linear and exponential regressions of annual 1969-79 catch per unit effort versus observed effort averaged over a 2-yr period for three species of thread herring captured on the Pacific coast of Costa Rica.

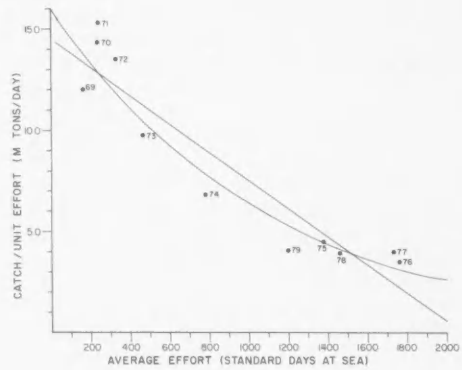

FIGURE 6.—Linear and exponential regressions of annual 1969-79 catch per unit effort versus standardized effort averaged over a 2-yr period for three species of thread herring captured on the Pacific coast of Costa Rica. Effort was standardized to account for improved capture efficiency and reduced resource availability after 1973 (see text).

effects on effort at Y_s, the exponential model produced higher f_s estimates, but only significantly with observed effort data.

Using "goodness of fit" as the only criterion, the most acceptable Y_s estimate was 6,430 t. This Y_s was surpassed by 760 t in 1974 and by 1,160 t in 1975. Catch remained at this maximum equilibrium level in 1976 and 1977, but declined to the pre-1974 level in 1978 and 1979. In fact, all the yield analyses except the linear model as applied to standardized CPUE and effort data indicated overfishing in 1974 and 1975.

According to the "best" unadjusted f_s estimate (1,036 d), fishing effort in 1975 abruptly exceeded—by 20%—the level which produced the maximum equilibrium catch and remained excessive in 1976 and 1977. Observed effort declined dramatically after 1977. Using standardized effort as a guide, the most acceptable f_s estimate (1,096 standard days) was exceeded by an average annual amount of 57% during 1975-77. Assuming that the standardization procedure was accurate, "real" effort remained slightly above 1,100 standard days in 1978 and 1979 even though catches were considerably below the estimated Y_s of 6,430 t. The exponential model predicted that the maximum equilibrium yield would be maintained when CPUE was 6.1 t/d or 5.9-6.0 t/standard day. The linear model predicted considerably higher Y_s/f_s values.

A comparison of the predicted yield curves for both models—as applied only to average observed and standardized effort—with actual 1969-79 catches (Figures 7, 8) revealed a closer overall agreement between catch and predicted yields for the exponential model even though the linear model produced a closer agreement for certain

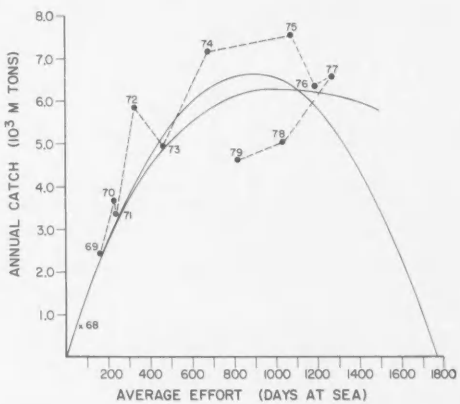

FIGURE 7.—Costa Rican thread herring yield curve predicted by the exponential and linear surplus production models and annual 1968-79 catch and average observed effort data.

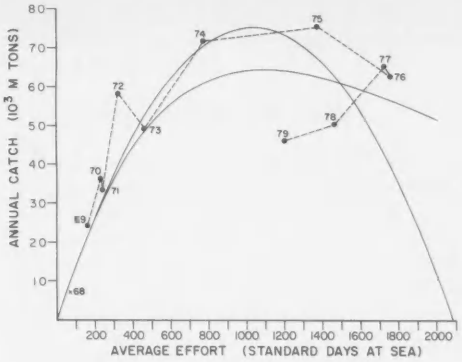

FIGURE 8.—Costa Rican thread herring yield curves predicted by the exponential and linear surplus production models and annual 1968-79 catch and average standardized effort data.

years. Catches in 1972, 1974, and 1975 were considerably greater than Y_E values estimated by the exponential model. The linear model predicted actual yields more accurately through 1975, especially when effort data were standardized, but deviated substantially in 1976 and 1977.

The general tendency toward increasing effort ceased in 1978 and 1979 when substantially lower catches were taken with less effort (Figures 7, 8). Linear and exponential models were fit to 1969-77 data, using average effort only, since it appeared that a closer agreement between observed and predicted yields might be obtained if data for the last 2 yr were eliminated. This was not the case. Y_s estimates increased by 280-360 t and f_s estimates by about 50 d (Table 8), corresponding to a slight shift upwards and to the right in the predicted yield curves, but no statistical improvement in fit could be demonstrated. Yield analyses therefore were quite robust since approximately the same results were obtained from the two data sets.

TABLE 8.—Estimates of maximum equilibrium yield (Y_s), the corresponding amount of fishing effort (f_S) and Y_S/f_S estimates for the Costa Rican thread herring fishery as derived from linear and exponential surplus production models for 1969-76. Only average observed and adjusted effort data were used.

Model	Effort	Y_S[1] (t)	f_S (d at sea)	Y_S/f_S (t/d)	F-statistic
Linear	Observed	7,050	930	7.58	54.7
	Adjusted	7,910	[2]1,090	7.26	49.1
Exponential	Observed	6,570	1,075	6.11	124.8
	Adjusted	6,780	[2]1,149	5.90	138.2

[1]Rounded off to the nearest 10 t.
[2]Effort expressed in standard days at sea.

Evaluation of the Model

A fundamental assumption of the surplus production yield model is that surplus population growth that is harvested by the fishery is at any point in time a function of population biomass. Under the assumption that fishing mortality is directly related to fishing effort by a constant proportionality factor, changes in the rate of population growth can also be related to fishing effort. Thus, the model assumes equilibrium conditions, i.e., that changes in population size—as estimated by CPUE—will remain in equilibrium with a given fishing effort. For developing fisheries in which effort is continually increasing, this equilibrium seldom has an opportunity to become established. Even in cases where effort does stabilize, variations in population size (and therefore, yields) can be expected, especially if recruitment is highly variable and bears little relation to spawning stock size. The problem is further exacerbated if there is a significant delay between spawning and recruitment since the model assumes that the response of equilibrium yield to changes in population size is immediate. In fact, yield in any given year will seldom be related to population size during the same year.

For the Pacific thread herring, the presumed lag time between spawning and recruitment was small (1 yr?) and correction procedures were not employed. The relationship between recruitment and stock size for *Opisthonema* spp. was not known, but the fact that the Costa Rican thread herring population declined without major interruptions once the fishery began suggests that recruitment fluctuations were not extreme. If recruitment had varied significantly as stock size declined, the reduction in CPUE with increasing effort (Figures 5, 6) would not have been so uniform and the model would not have fit the data nearly so well.

A major problem which is common to all surplus production yield analyses is the nonindependence of X and Y variables when CPUE is plotted as a function of effort. As pointed out by Sissenwine (1978), the relationship between X and its reciprocal is hyperbolic. Therefore, CPUE vs. effort relationships are inherently biased. Following Gulland's (1969) procedure for averaging effort in the independent variable, not only does the model

more closely approximate equilibrium conditions, but the replacement of f_t by $\bar{f}$ reduces the interdependence of the two variables. However, as demonstrated by Roff and Fairbairn (1980), temporal trends in effort such as those observed for the Costa Rican thread herring fishery produce correlations between f_t and $\bar{f}$ since both are increasing (or decreasing). This autocorrelation in the independent variable in turn indicates a spurious correlation between CPUE and average effort. In the examples examined by those authors, the degree of autocorrelation between f_t and $\bar{f}$ increased when shorter time periods were used to calculate $\bar{f}$. Furthermore, for periods of 2 or 3 yr, there was a significant correlation between f_t and $\bar{f}$ even in the absence of trends in f_t over time.

In the present assessment, since there were definite trends in both standardized and unstandardized effort and since effort was averaged over only a 2-yr period, the nonindependence of the variables in the regression analyses could not have been significantly reduced. In fact, an examination of the deviations between observed and predicted CPUE for both models as applied to average observed and standardized effort (Figure 9) revealed considerable time trends. These trends were more obvious after effort standardization. Clearly, the variables in the regression analyses were not independent. Strictly speaking, therefore, the F-test used to evaluate the degree of fit was not valid since it assumes that Y observations are independent and normally distributed with common variance. Residual mean squares for the individual regression analyses, however, assume nothing about the distributive properties of the error term in the regression model. Although they cannot be used to evaluate the statistical significance of fit, they did confirm that better fits were obtained with average effort, the exponential model and standardized effort.

A second problem which was not addressed was the assumption that fishing mortality remained directly proportional to fishing effort (Equation (3)) as population size diminished. Thread herring may remain vulnerable to capture even at low stock sizes since they congregate in schools at the surface, i.e., the same fishing mortality may be exerted even with reduced effort. If fishing mortality and effort do not remain directly proportional, the surplus production model is not appropriate for predicting maximum equilibrium yields. There was no way to evaluate this possible source of error.

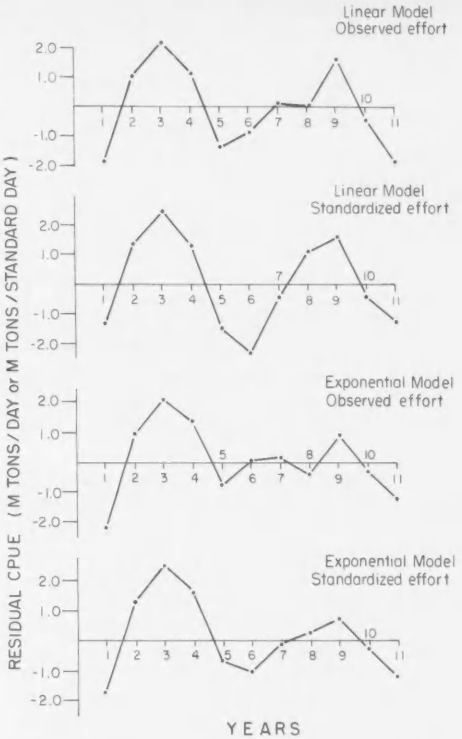

FIGURE 9.—Residual (observed-predicted) 1969-79 catch per unit effort values for the linear and exponential yield models arranged in chronological sequence.

Despite these problems, the surplus production model provided a clear analytical interpretation of the data. The range of Y_s and f_s estimates was not extreme, although the linear model applied to standardized data produced higher Y_s estimates than the other analyses. While there was no basis for assessing how "correct" the standardization procedure was, it did result in higher Y_s and f_s estimates for both the linear and exponential models and improved the least squares fit to the data, especially for the exponential model. Clearly, some adjustment in observed effort was called for. Acceptable estimates of Y_s and f_s were obtained from a fairly short time series of catch and effort data (11 yr). The success of this assessment was due in part to the reliability of the catch and effort data provided by the canning companies to the Ministry of Agriculture, and the fact that data

were available from the beginning of the fishery as well as from the period characterized by diminishing yields.

Management Implications

This assessment of the Costa Rican thread herring resource indicated that a maximum equilibrium yield of approximately 6,430 t was surpassed in 1974-75, leading to stock depletion and reduced catches in subsequent years. Declining catches during 1976-79 were certainly due only in part to reduced effort. Effort increased dramatically after 1973 and remained in excess of f_s (1,036 d) during 1975-77. "Real" effort may have remained slightly above optimum even in 1978 and 1979 when catch declined to about 5,000 t.

Management thus far has been self imposed by the industry in response to rapidly declining CPUE. Economic returns have presumably suffered at least as much as biomass yields. To protect the resource, Costa Rican Government regulation would only be necessary if effort again approached 1,000 d at sea or if catch exceeded 6,500 t. Regulation of effort should concentrate on "real" effort, not merely the number of days vessels spend at sea. It would be important, therefore, to maintain effort at some level below 1,000 d if fishing power were suddenly increased, say, by the use of aircraft to spot schools of fish. Since real effort is not easily measured, a catch quota might be a more practical management strategy. Given the small number of vessels in the fishery, allocation of vessel quotas would be feasible. A reduction in the number of vessels, however, would more effectively maintain acceptable economic returns for the industry. Maximum economic returns would presumably be achieved at some effort level below f_s.

Once an exploited population is depleted, biomass can be restored to a level which supports maximum equilibrium yield by reducing the harvest of adults, thus reducing adult mortality and stimulating increased recruitment. Catch should be maintained at reduced levels for a period of time equal to the delay between spawning and recruitment. As a general policy, fishing at below Y_s also protects to some extent against additional stock depletion due to poor recruitment. For the Costa Rican thread herring population, some increase in stock size (and therefore CPUE) following overfishing in 1974-75 should have been noticeable after a year or two of reduced catches such as occurred in 1978-79. The observed increase in CPUE since 1976 (Table 2, Figure 2) was small and may not have been "real" since standardized CPUE stabilized after 1976 (Table 6). However, catch and effort data available for the first 5 mo of 1980 (Table 9) showed a continued low CPUE when compared with the same period in 1979.

TABLE 9.—Observed catch, effort, and CPUE data compiled from sales receipts for the first 5 mo of 1979 and 1980 for thread herring captured on the Pacific coast of Costa Rica. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Period	Catch (t)	Effort (d at sea)	CPUE (t/d at sea)
Jan.-May 1979	2,270	330	6.88
Jan.-May 1980	1,860	340	5.47

Unit stock identification is an important area requiring further research. Although thread herring on the Pacific coast of Central America may not be highly migratory, it seems likely that there is some mixing across national boundaries. The rapid decline in population size in Costa Rican waters—as inferred from reduced CPUE estimates—would not have been possible, however, if there had been a significant influx of fish from other areas along the Central American coastline. The Panamanian thread herring fishery is only active in the Gulf of Panama, although thread herring were detected acoustically in the Gulf of Chiriqui (see Figure 1) and off Guatemala, El Salvador, and Nicaragua during a 1970 survey (Magnusson 1971). If the same stock is presently being exploited in Costa Rican and Panamanian waters, stock assessment and resource management should be a joint activity of both countries. The possibility also exists that more than one stock is present in Costa Rican waters, either geographically or taxonomically. Clearly, the assumption that the three species which currently make up the catch can be treated as a single unit stock needs to be confirmed with additional ecological and life history information. In the meantime, efforts should be made to determine the species composition of landings, and to compile catch and effort data by species.

SUMMARY

1. Catch and effort data were compiled for three species of Pacific thread herring harvested in Costa Rican waters during 1968-79. Effort was estimated as the number of calendar days at sea. Data were available from the beginning of the

fishery and from a period of diminishing and declining yields.

2. Effort data were standardized to account for a presumed 25% increase in capture efficiency beginning in 1974 when larger, more powerful vessels with larger nets first entered the fishery and for a presumed 5% annual increment in the proportion of time spent searching for fish as stock size declined beginning in 1975.

3. Estimates of maximum equilibrium yield (Y_s) were obtained by fitting linear and exponential forms of the surplus production model to plots of catch per unit effort (CPUE) vs. effort. Eight yield analyses were performed using observed and standardized effort to calculate CPUE and a moving 2-yr average of observed and standardized effort as well as simple annual observed and standardized effort as the independent variable.

4. All regression analyses were statistically significant at the 99% confidence level. The standardization and averaging of effort data, and the use of the exponential model improved the degree of statistical fit. The predicted yield curves fit observed catch data fairly well.

5. Y_s estimates ranged from 6,290 to 7,890 t, observed f_s ranged from 888 to 1,067 d and standardized f_s ranged from 1,041 to 1,117 standard days. The best fit to the data was obtained with the exponential model applied to standardized CPUE vs. average standardized effort data. This analysis produced a Y_s estimate of 6,430 t and a f_s estimate of 1,096 standard days. The best estimate of unstandardized effort was 1,036 d.

6. The "best" Y_s estimate was exceeded by 760 t in 1974 and by 1,160 t in 1975. Overfishing probably contributed to catches of 5,000 t and lower in 1978-79. Observed effort abruptly exceeded f_s in 1975 by 20%, remained above 1,000 d in 1976 and 1977, and then declined dramatically in 1978-79. Standardized effort remained slightly above standardized f_s even in 1978 and 1979.

7. Attempts to reduce the dependence of the CPUE and effort variables in the regression analyses by averaging effort were of doubtful value since there was a trend toward increasing effort as the fishery developed and since only 2 yr were used to average effort. Thus, significant autocorrelations between f_s and $\bar{f}$ could not be avoided. Obvious time trends in the deviations between predicted and observed CPUE provided evidence for the nonindependence of the variables in the regression analyses. This problem, however, was not believed to have seriously altered the results of the assessment.

8. The industry should be encouraged to either maintain effort below 1,000 d at sea or annual catch below 6,500 t as was done in 1978 and 1979. If regulations are necessary, a catch quota may prove to be more feasible since it could fairly easily be allocated to individual vessels and since effort limitations must consider "real" changes in fishing effort which are difficult to quantify. On the other hand, a reduction in the number of vessels would improve economic returns for the fishing vessels which remain in the fishery.

9. Unit stock identification is an important area requiring further research. The inferred rapid reduction in stock abundance in Costa Rican waters suggests that there was little net immigration of thread herring from neighboring countries, but the degree to which the stock (or stocks) exploited by the Costa Rican fleet may also be exploited elsewhere (Panama, in particular) needs to be clarified.

ACKNOWLEDGMENTS

The authors wish to thank the vessel captains and the owners and managers of the three Costa Rican canning companies for their cooperation; the biologists, assistant biologists, and statisticians of the Ministry of Agriculture Fisheries Office in Puntarenas, Costa Rica, for compiling catch and effort data; and to Eduardo Bravo, Milton Lopez, and Eduardo Lopez of the Ministry of Agriculture Fisheries Resources and Wildlife Division, San Jose, Costa Rica, for their encouragement and support. Thanks are also extended to Adan Chacon of the Costa Rican Ministry of Agriculture and David Sampson of the Maine Department of Marine Resources for their assistance with mathematical and statistical procedures and to four anonymous reviewers for their constructive criticism.

LITERATURE CITED

BERRY, F. H., AND I. BARRETT.
1963. Gillraker analysis and speciation in the thread herring genus *Opisthonema*. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 7:111-190.

BEVERTON, R. J. H.
1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 154:44-67.

FOOD AND AGRICULTURE ORGANIZATION.
1979. Catches and landings, 1978. FAO, Yearb. Fish. Stat. 46, 372 p.

FOX, W. W., JR.
1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99:80-88.

FUSS, C. M., JR., J. A. KELLY, JR., AND K. W. PREST, JR.
1969. Gulf thread herring: aspects of the developing fishery and biological research. Proc. Gulf Caribb. Fish. Inst. 21:111-125.

GRAHAM, M.
1935. Modern theory of exploiting a fishery, and application to North Sea trawling. J. Cons. 10:264-274.

GULLAND, J. A.
1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO Man. Fish. Sci. 4, 154 p.

HOUDE, E. D.
1976. Abundance and potential for fisheries development of some sardine-like fishes in the eastern Gulf of Mexico. Proc. Gulf Caribb. Fish. Inst. 28:73-82.

KINNEAR, B. S., AND C. M. FUSS, JR.
1971. Thread herring distribution off Florida's west coast. Commer. Fish. Rev. 33(7-8):27-39.

KLIMA, E. F.
1971. Distribution of some coastal pelagic fishes in the western Atlantic. Commer. Fish. Rev. 33(6):21-34.

MAGNUSSON, J.
1971. Pacific coast pelagic survey off Central America and Panama Bay, June 1970-January 1971. Proj. Reg. Desarr. Pesq. Centro-Am. Bol. Tec. IV(6), 32 p.

MURPHY, G. I.
1977. Characteristics of clupeoids. *In* J. A. Gulland (editor), Fish population dynamics, p. 283-308. Wiley, N.Y.

PETERSON, C. L.
1956. Observations on the taxonomy, biology and ecology of the engraulid and clupeid fishes in the Gulf of Nicoya, Costa Rica. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 1:137-280.

PRISTAS, P. J., AND R. P. CHEEK.
1973. Atlantic thread herring (*Opisthonema oglinum*) - movements and population size inferred from tag returns. Fish. Bull., U. S. 71:297-301.

ROFF, D. A., AND D. J. FAIRBAIRN.
1980. An evaluation of Gulland's method for fitting the Schaefer model. Can. J. Fish. Aquat. Sci. 37:1229-1235.

SCHAEFER, M. B.
1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter-Am. Trop. Tuna Comm., Bull. 1:25-56.

SISSENWINE, M. P.
1978. Is MSY an adequate foundation for optimum yield? Fisheries 3(6):22-24, 37-38, 40-42.

DIEL-DEPTH DISTRIBUTION OF SUMMER ICHTHYOPLANKTON IN THE MIDDLE ATLANTIC BIGHT

ARTHUR W. KENDALL, JR.[1] AND N. A. NAPLIN[2]

ABSTRACT

A series of discrete depth plankton tows made every 3 h over a 72-h period off Ocean City, Maryland, in July 1974 allowed analysis of the diel-depth distribution of ichthyoplankton. Overall egg and larval densities averaged 5.6 eggs/m^3 and 6.3 larvae/m^3. Seven species of eggs made up over 90% of those caught with *Merluccius bilinearis* eggs accounting for 45.9% of the eggs taken. Over 16 species of fish larvae were identified, of which *Urophycis* sp., *Pomatomus saltatrix*, and *Citharichthys arctifrons* were the most abundant. The fish eggs were concentrated near the surface and their age distribution at different times of day provided information about diel spawning times, spawning depth, and embryonic mortality. Larvae of all species moved to shallower depths at night. The actual depth distribution and extent of vertical movements varied among the species. The surface and the thermocline were the primary water column features to which diel movements were related.

Studies of the diel vertical distribution of early stages of fish contribute to knowledge of several phases of their life history. For eggs, diel and depth differences in age distribution can be used to estimate time of day and depth of spawning and hatching, rate of embryonic development, and to some extent egg mortality. For larvae, a large body of literature has confirmed the conclusions of the early work by Russell (1926) and Bridger (1956) that most species exhibit diel vertical migrations. Although the depth ranges differ, most species move to shallower depths at night. In some species, e.g., herring, *Clupea h. harengus*, (Seliverstov 1974) and yellowtail flounder, *Limanda ferruginea*, (Smith et al. 1978) the extent of movement increases as the larvae grow. Speculation about causes of vertical migration has centered around diel feeding behavior and predator avoidance. Most larval fishes are visual feeders on zooplankters, which undertake vertical migrations similar to those of larval fish. In addition, Zaret and Suffern (1976) concluded that vertical migration patterns occur in prey species that are vulnerable to visually dependent predators; thus, larvae may reduce predation by moving to deeper water during the day.

Aside from understanding the biological consequences of vertical distribution of larval fishes, the effect this distribution has on results of broad-scale ichthyoplankton surveys is critical. During most such surveys, samples are taken at more-or-less random times during a 24-h day at stations that are separated by tens of kilometers. Depending on the sampling procedures, the diel spawning and embryonic developmental cycle and the diel vertical distribution of larvae may affect interpretation of catches from surveys (Ahlstrom 1959; Miller et al. 1963). If sampling fails to include the entire depth range of the taxa sought, errors in abundance estimates will be made.

METHODS

After making several trial tows at varying distances from shore between Sandy Hook, N.J., and Ocean City, Md., we located a concentration of fish larvae 95 km off Ocean City (lat. 38°32′ N, long. 73°52′ W) in 57 m of water (Figure 1). Earlier studies (Kendall and Walford 1979) indicated that larvae of bluefish, *Pomatomus saltatrix*, which were among those found here, occurred primarily near the surface, above the thermocline. To track the concentration of larvae we deployed a parachute drogue with a lighted staff buoy and the parachute centered at 5-10 m in the layer above the thermocline which was present from 10 to 30

[1]Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, N.J.; present address: Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2]Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, N.J.; present address: 613 Riverbend Drive, Fort Collins, CO 80524.

Manuscript accepted May 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

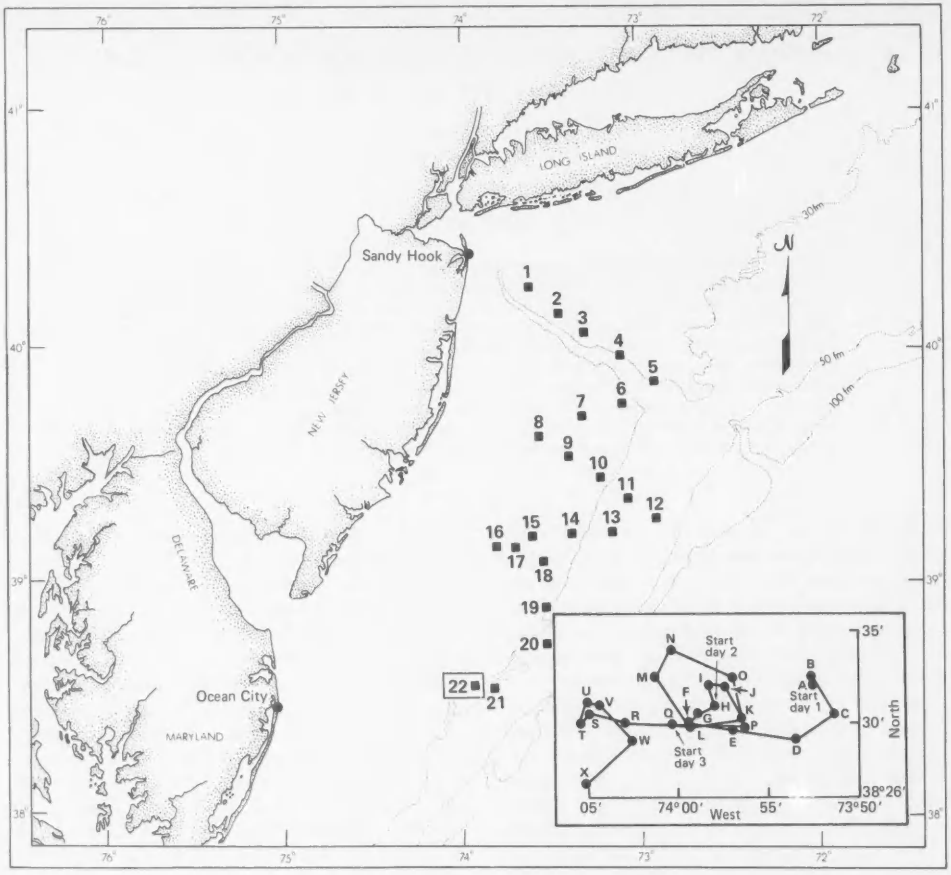

FIGURE 1.—Search (squares) and drogue stations (inset) during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

m. Plankton was sampled near the drogue at 3-h intervals for 72 h starting at 0600 (e.s.t.) on 18 July 1974. We used 20 cm bongo nets equipped with General Oceanics[3] flowmeters and 0.505 mm mesh nets. This mesh size may have caused extrusion of smaller larvae and eggs. Two or four nets were fished simultaneously at discrete depths. A Braincon 6-ft (1.82 m) V-fin depressor was used and wire stops held the nets at predetermined places on the wire.

Before each tow, temperature profiles were obtained with expendable bathythermographs and surface salinity samples were taken. Before every other haul salinity samples from the sampling depths and 50 m were obtained. Salinities were determined on shore with a Beckman RS 7B induction salinometer.

Nominal plankton sampling depths were: surface, 2, 4, 6, 15, and 30 m. Every 3 h a haul was made at 0, 4, 15, and 30 m (first experiment). During the second half of the 72-h period, on every other haul a second haul was made in a similar manner immediately after the first one with the

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

nets fishing at 2 and 6 m (second experiment). The depth stratum from 30 m to the bottom (57 m) was not sampled, and some larvae probably occurred in this area. Bendix bathykymographs on the wire near the subsurface nets checked the actual sampling depths on each haul. During each haul we placed the nets on the wire as it was paid out; the vessel maintained minimal headway to keep the nets from tangling around the wire. Once the nets were on the wire, the vessel speed was increased to 5 kn (9.3 km/h). Hauls lasted 15 min from the time the surface net started to fish to when it was brought out of the water. At the end of the 15 min, the ship was set adrift and the nets were hauled in as quickly as possible. Since the nets had no opening-closing devices, this procedure minimized contamination of the deeper nets by organisms in shallower water. Such contamination was considered inconsequential since the horizontal towing distance was a nominal 2,325 m, and maximum towing distance in shallower layers for the 30 m net was judged to be 75 m (3.2% of the haul); however, it may have accounted for some of the predominantly shallow-caught larvae found in the deeper nets. Samples were preserved in 5% seawater buffered Formalin. The bongo nets provided paired samples that we designated port and starboard. All starboard net samples and one of the four or six port net samples from each sampling time were brought ashore. All fish eggs and larvae were removed from the plankton samples, identified, and counted.

Selected samples of Atlantic whiting,[4] *Merluccius bilinearis*; Gulf Stream flounder, *Citharichthys arctifrons*; and snake eel, *Pisodonophis cruentifer*, eggs were staged (categorized according to developmental stage), based on divisions of the embryonic period used by Naplin and Obenchain (1980). Although many of the early stage eggs had ruptured yolks, these were considered intact prior to sampling. As has been noted in other species (Leis 1977), until the blastoderm completely covers the yolk sac, yolk breakage occurs easily and is likely to happen during sampling. Some middle stages, too, were ruptured, but we cannot determine whether they ruptured during sampling or whether they were already dead when collected. As most of the embryos looked normal and undeteriorated other than having a ruptured yolk, these also were considered to have been alive when sampled.

Atlantic whiting eggs were initially staged at all depths for the first day of sampling (39 samples at eight time periods). Predominant stages at a particular time of day were the same regardless of depth, indicating that stages were not stratified with depth. As 95% of the eggs were taken in the surface and 4 m samples, only the surface samples were staged at each time period for the remaining 2 d of sampling. Gulf Stream flounder eggs were staged at all depths for the first day of sampling, and snake eel eggs, which occurred in fewer numbers, were staged at all depths for all 3 d of sampling.

Stokes' law for determining the settling velocity of a particle has been used to estimate the rising velocity of planktonic eggs (English 1961). Stokes' law, applied to this problem states that

$$V = \frac{2}{9} g \frac{[d_1 - d_2]}{\mu} r^2$$

where V = velocity
d_1 = density of egg
d_2 = density of liquid
g = acceleration of gravity
r = radius of egg
μ = dynamic viscosity of liquid.

All values are expressed in the centimeter-gram-second system. Although no measurements of specific gravity of eggs for species discussed here are available, values for other planktonic eggs have ranged from 1.021 for pleuronectid eggs (English 1961) and for eggs of the gadid *Theragra chalcogramma* (Kanoh 1954) to 1.0287 for *Argentina silus* eggs (Schmidt 1906, quoted by Breder and Rosen 1966). We used the 1.021 value in our calculations because a value >1.022 would not permit eggs to float in the upper 10 m where the eggs we took were abundant.

Bluefish larvae from all samples were measured and those from a subset of 28 samples were used for gut content analysis. From each of these samples, 10 fish representing the sample size distribution were examined for gut contents. The number and types of food organisms in the foregut, midgut, and hindgut were noted. Atlantic whiting and Gulf Stream flounder larvae were also measured.

[4]The common name Atlantic whiting is used in this paper for *Merluccius bilinearis* to avoid confusion with hakes (*Urophycis* spp.). Recently the common name of *M. productus* has been changed from Pacific hake to Pacific whiting. We suggest that fish of the genus *Merluccius* be recognized as whitings, a name in common use on the east coast already.

The average volume of water filtered during the hauls was 82.9 m^3 (range 58.6-109.2 m^3). All numbers of eggs and larvae were adjusted to numbers per 100 cubic meters. Using UCLA BMD computer program 02V (Dixon 1973), analyses of variance were performed for several species after the data had been transformed to $\log_{10}(X + 1)$ to normalize the distribution and homogenize the variances, which were proportional to the means before transformation. The factorial design of the first experiment had the following factors: three 24-h days, four sampling depths (0, 4, 15, 30 m), and day and night. Each factor combination had three replicates. Because the cruise was in mid-summer, by sampling every 3 h, three tows were taken each night and five each day. To equalize the number of day and night tows for the analyses of variance, only the first, third, and fifth daytime tows were used. We performed similar analyses on the data associated with the second experiment when collections were also made at the 2 and 6 m depths. For these data the factors were: three times of day (evening—1800 h; night—0000 h; and day—0600 h and 1200 h), and six depths (0, 2, 4, 6, 15, 30 m). Each of these factor combinations had two replicates.

RESULTS

The drogue drifted about 11 nmi (20.4 km) to the west-southwest of its original position during the 72-h sampling period. Three circular patterns that corresponded to a diurnal tidal cycle were evident within the overall drift (Figure 1). During the first half of the experiments the wind was generally southerly at 5-25 kn (9.3-46.3 km/h). The skies were cloudy and a thundersquall occurred around 0300 h on the first night. Around 2100 h on the second night there was another thundersquall, and at 0300 h the wind shifted to north-northwest at 20 kn (37.0 km/h) and the skies cleared. The wind diminished during the third day and by 2100 h it had shifted to southeast at only 2 kn (3.7 km/h). The sky remained clear. The sun rose at 0545 h and set at 2016 h during the experiments. The new moon rose and set during twilight or daylight hours throughout the sampling period, so there was no moonlight at night.

The water column represented three water types characteristic of the continental shelf of the Middle Atlantic Bight. Coastal water above the thermocline at 8 m was isothermal at 22.2°-22.8° C and had salinities of <33.6‰ (Figure 2). Below

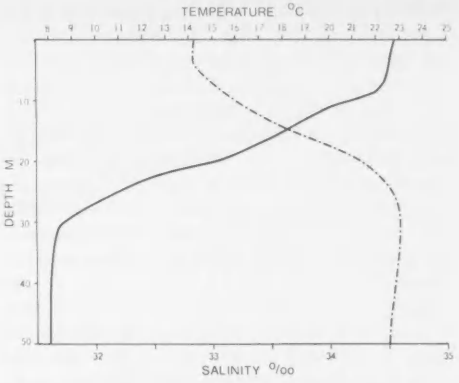

FIGURE 2.—Mean temperature (line) and salinity (dashed line) profiles at drogue stations during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

the thermocline, where temperatures dropped from 21.5° C at 10 m to 8.5° C at 30 m and salinities exceeded 33.6‰, was shelf edge water (Wright and Parker 1976). Near the bottom, where temperatures were <10° C and salinities were 34.5-34.6‰, the water was part of the cool pool that occurs over the middle of the shelf off the Middle Atlantic Bight in summer (Bowman and Wunderlich 1977). The diversity of ichthyoplankton collected was probably due in part to our sampling in these three water types.

A total of 61,534 eggs (an overall arithmetic mean of 562 eggs/100 m^3), most of which were identified to species, were taken during the experiments (Table 1). Most numerous were Atlantic whiting and Gulf Stream flounder. Butterfish, *Peprilus triacanthus*; fourspot flounder, *Hippoglossina oblonga*; hakes, *Urophycis* spp.; snake eel; and cunner, *Tautogolabrus adspersus*, eggs were also taken in significant numbers. No bluefish eggs were taken during the cruise.

Throughout the cruise, egg numbers of all species decreased with depth. Data from the second experiment was similar to that from the first, and showed that the catches at 6 m more closely resembled those at the surface and 4 m than those at 10 and 30 m. These findings indicate that the planktonic eggs of all species taken behave in much the same way in the water column, and have similar specific gravities.

A total of 68,840 larvae (an overall mean of 629 larvae/100 m^3), of which most were identified to

TABLE 1.—Numbers and relative abundance of fish eggs and larvae at the drogue stations during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Taxon	Eggs			Larvae		
	Total number	Mean no./ 100 m³	% of total	Total number	Mean no./ 100 m³	% of total
Hakes, *Urophycis* spp.	2,988	27	4.9	15,972	146	23.2
Bluefish, *Pomatomus saltatrix*				15,202	139	22.1
Gulf Stream flounder, *Citharichthys arctifrons*	17,311	158	28.1	13,568	124	19.7
Frigate mackerel, *Auxis* sp.				5,904	54	8.6
Butterfish, *Peprilus triacanthus*	4,497	41	7.3	5,445	50	7.9
Fourspot flounder, *Hippoglossina oblonga*	3,898	36	6.3	5,062	46	7.4
Atlantic whiting, *Merluccius bilinearis*	28,243	258	45.9	3,281	30	4.8
Smallmouth flounder, *Etropus microstomus*				1,000	9.1	1.5
Atlantic bonita, *Sarda sarda*	114	1.0	.2	764	7.0	1.1
Searobins, *Prionotus* spp.				445	4.1	.6
Cusk eels, Ophidiidae				183	1.7	.3
Cunner, *Tautogolabrus adspersus*	2,397	22	3.9	152	1.4	.2
Yellowtail flounder, *Limanda ferruginea*				151	1.4	.2
Eels, Anguilliformes				98	.9	.1
Goosefish, *Lophius americanus*				63	.6	.1
Witch flounder, *Glyptocephalus cynoglossus*				42	.4	.1
Snake eel, *Pisodonophis cruentifer*	2,058	19	3.3			
Miscellaneous[1]	28	.3		1,508	13.8	2.2
Total	61,534	562	99.9	68,840	629	100.1

[1]Animals that were too mutilated to be identified or too sparse for meaningful analysis.

species, were taken during the experiments (Table 1). Hakes, bluefish, and Gulf Stream flounder were most abundant, and frigate mackerel (*Auxis* sp.), butterfish, fourspot flounder, Atlantic whiting, and smallmouth flounder, *Etropus microstomus*, were taken in substantial numbers.

Bluefish

An overall mean catch of 139 larvae/100 m³ was made placing bluefish second to hakes in abundance. A highly significant difference occurred in the catches among the 3 d, with more larvae caught on day 2 than on the other 2 d (Table 2). More larvae were taken in the surface and 4 m nets than at other depths, with more taken at the surface at night than during the day (Figures 3, 4). Both day and night catches at 15 and 30 m were so small that they may have been a result of contamination of the nets as they passed through shallower water. During the second experiment, the larvae were concentrated at 2 m at night and 6 m at other times (Table 2).

The vertical-diel migration of these larvae is clearly seen by comparing the proportions of larvae in the 0 and 4 m tows at each time of day sampled (Figure 4). The proportion in the surface tow was lowest at midday (1200 h) when it was 4% of the total catch. It increased steadily to 49% of the catch at midnight (0000 h) when it started to decline again, reaching 17% by midmorning (0900 h). Thus the larvae appear to be varying their depth distribution continuously on a diel cycle, concentrating near 4 m during midday and at the surface at night.

The percentage of the larvae with food in their guts also showed a marked diel pattern (Figure 4). The maximum proportions of larvae with food in their guts were taken from 0600 to 1200 h when 86-90% of the guts contained food. At 1500 and 1800 h, 70% of the larvae contained food. By 2100 h the proportion had dropped to 22% and during the night (0000 and 0300 h) none of the larvae had food in their guts.

Most of the food consisted of various life stages of copepods, including nauplii, copepodites, and adults. Cladocerans and invertebrate eggs were also present in small numbers. It also appeared that smaller larvae had higher proportions of nauplii while larger larvae had higher proportions of adult copepods and cladocerans although too few fish were examined for detailed analysis.

Several factors indicate that food passes through the gut fairly rapidly. Few fish had any food particles in the foregut. At 0600 h about twice as many larvae had food in the midgut as had food in the hindgut. Later in the day about equal numbers of larvae contained food in the midgut and in the hindgut. At no time did more hindguts than midguts contain food.

The mean lengths of bluefish larvae were compared among the tows. The mean length for all tows was 4.33 mm (Table 3). We found no significant difference in mean lengths among the 3 d of sampling, between day and night sampling, or among the six sampling depths. Larger larvae

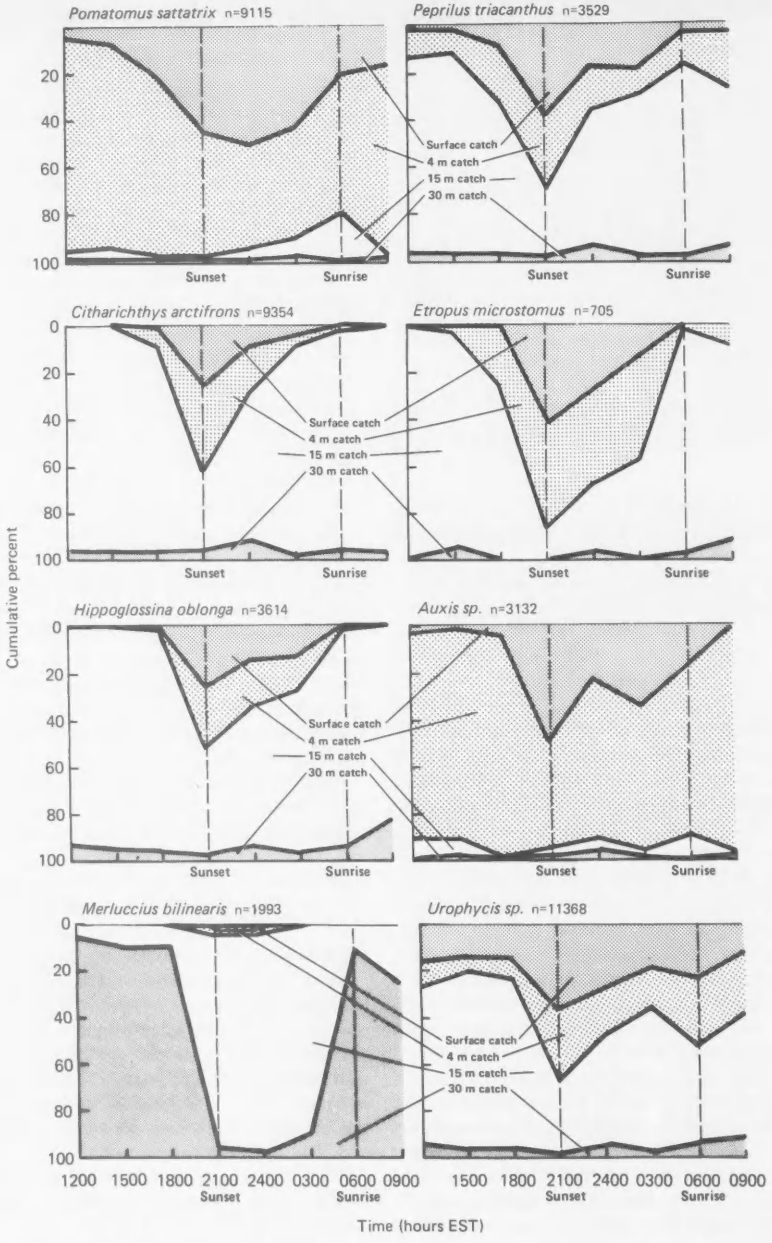

FIGURE 3.—Mean proportions of larvae of eight species of fish at four depths over a 24-h cycle from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

TABLE 2.—Transformed ($\log_{10} X + 1$) mean numbers of larvae per 100 m^3 and *F*-values from analysis of variance for eight species of fish taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Item	Bluefish	Atlantic whiting	Gulf Stream flounder	Butterfish	Fourspot flounder	Hakes	Frigate mackerel	Smallmouth flounder
Experiment 1: depths = 0, 4, 15, 30 m; times = day, night; days = 1, 2, 3								
Means:								
Overall	1.550	0.786	1.311	1.315	1.088	1.904	1.056	0.524
Day	1.497	.692	1.105	1.222	.799	1.885	.880	.392
Night	1.603	.880	1.518	1.408	1.378	1.923	1.233	.656
Day 1	1.289	.819	1.215	1.334	1.024	1.945	.793	.199
Day 2	1.717	.879	1.287	1.287	1.006	1.859	1.238	.538
Day 3	1.644	.660	1.432	1.325	1.235	1.907	1.138	.835
Depths:								
0	1.847	.150	.835	1.087	.791	2.005	1.222	.445
4	2.375	.266	1.075	1.400	.846	1.916	1.870	.658
15	1.210	1.404	2.193	1.391	1.849	2.378	.728	.801
30	.768	1.323	1.143	.843	.867	1.318	.405	.191
F-values								
Days	12.32**	3.77*	1.32	.09	3.33*	.43	11.45**	25.40**
Day-night (diel)	1.99	7.89**	13.72**	3.80	51.63**	.26	19.74**	13.22**
Depth	88.13**	99.32**	29.19**	24.14**	39.88**	33.74**	64.43**	13.31**
Days/Day-night	1.35	3.49*	.40	.20	.72	.54	2.53	5.58**
Days/Depth	1.02	.13	1.20	1.06	3.65**	1.10	2.06	2.70*
Day-night/Depth	6.96**	4.88**	13.49**	5.70**	29.57**	2.85*	6.89**	13.16**
Days/Day-night/Depth	1.72	.30	.81	.42	1.36	1.89	1.31	1.80
Experiment 2: depths = 0, 2, 4, 6, 15, 30 m; times = 1800, 0000, 0600-1200 h								
Means:								
Overall	1.954	.523	1.280	1.348	1.073	1.909	1.422	.740
Times:								
1800	1.945	.524	1.388	1.570	0.818	1.810	1.521	1.019
0000	1.965	.591	1.612	1.375	1.458	1.892	1.598	.638
0600-1200	1.952	.453	.840	1.100	.942	2.023	1.146	.563
Depths:								
0	1.839	.064	.633	.864	.459	1.946	.941	.361
2	2.295	.115	1.308	1.362	1.223	2.000	2.026	.958
4	2.471	.244	.994	1.410	.615	1.847	1.931	.731
6	2.628	.244	1.154	1.552	1.043	2.016	2.179	.809
15	1.552	1.117	2.260	2.065	2.176	2.388	.984	1.288
30	.939	1.351	1.331	.817	.920	1.254	.468	.294
F-values								
Time of day	.02	.74	10.36**	12.02**	10.46**	2.25	7.69**	5.92
Depth	30.85**	2.48	9.73**	22.90**	16.80**	13.32**	33.32**	6.90**
Time/Depth	2.63*	8.54**	4.49**	5.08**	3.17*	1.27	3.89**	4.80**

*P = 0.05; **P = 0.01.

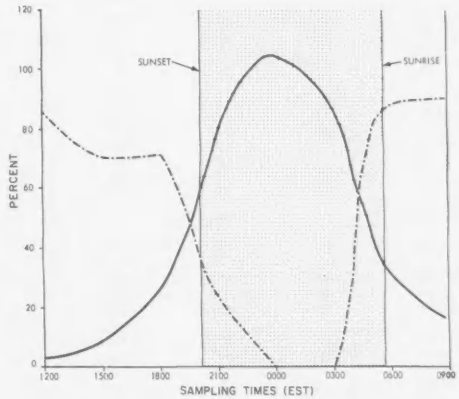

FIGURE 4.—Mean percentage (surface/4 m) of bluefish larvae in the 4 m tow relative to those in the 0 m tow (line) and percentage of bluefish larvae with food in their guts (dashed line) by time of day from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

TABLE 3.—Mean standard lengths (millimeters) of bluefish larvae taken at various times of day and depths during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Depth (m)	Day 1		Day 2		Day 3		All times
	Day	Night	Day	Night	Day	Night	
0	5.30	4.38	4.57	4.25	4.87	4.69	4.57
2			4.38	4.45	4.60	4.85	4.59
4	4.38	4.52	3.89	4.45	4.27	4.63	4.22
6			4.27	4.42	4.25	4.79	4.33
15	4.65	4.45	4.49	4.42	4.31	4.71	4.47
30	4.57	4.61	4.45	4.35	4.25	4.50	4.45
	Day 1 - 5.00		Day 2 - 4.18		Day 3 - 4.46		
	Day - 4.25		Night - 4.54		Overall - 4.33		

showed no increased net avoidance during daylight, nor any difference in depth distribution with size. The apparent lack of larval growth over the 72-h sampling period may be related to the difference between the drift of bluefish larvae and that of our drogue.

Since bluefish egg incubation takes about 48 h

at temperatures near 22° C (Salekhova 1959; Deuel et al. 1966) and bluefish larvae hatch at about 3.0 mm, the larvae we caught averaging 4.3 mm were probably several days old. Apparently bluefish spawned rather steadily over a period of several days somewhere "upstream" from our drogue a few days prior to our experiment, and the larvae drifted continuously through our sampling area. Alternate hypotheses that the larvae did not grow during the experiment, or that larvae >4.3 mm avoided the nets, do not seem as tenable.

Atlantic Whiting

Atlantic whiting eggs were the most numerous among the species taken, with an overall mean of 258 eggs/100 m^3 taken during the cruise. All three primary factors (depth, time of day, and days) showed significant differences: egg number decreased with increasing depth (Figure 5), more eggs were taken at night than during the day, and significantly fewer eggs were taken on the second sampling day than on the other two (Table 4).

The uneven distribution of various developmental stages over time allows separation of eggs into distinct groups or batches whose development can be traced from spawning through hatching (Table 5). At each sampling time, eggs from two distinct batches were taken which apparently represented the daily spawning products of adults in the area. Very early stages appeared daily in the afternoons from about 1500 to 1800 h. These eggs continued developing throughout the next day and began hatching at 0300 h the second day after being spawned. After 0900 h, virtually all eggs had hatched. Therefore, the total incubation time at the surface temperature we observed, 22.2°-23.2° C (mean = 22.7° C), was about 39 h.

TABLE 4.—Transformed ($\log_{10} X + 1$) mean numbers of eggs per 100 m^3 and *F*-values from analysis of variance for six species of fish taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Item	Atlantic whiting	Gulf Stream flounder	Butterfish	Fourspot flounder	Hakes	Snake eel
Experiment 1: depths = 0, 4, 15, 30 m; times = day, night; days = 1, 2, 3						
Means:						
Overall	1.971	2.059	1.180	1.228	1.056	0.907
Day	1.892	1.996	1.052	1.259	.985	.864
Night	2.051	2.122	1.307	1.197	1.128	.950
Day 1	2.058	1.888	1.090	.944	1.053	.831
Day 2	1.867	2.110	1.255	1.336	.998	.861
Day 3	1.988	2.179	1.194	1.403	1.119	1.029
Depths:						
0	2.640	2.251	1.575	1.677	1.521	1.271
4	2.606	2.205	1.670	1.685	1.582	1.494
15	1.552	1.887	.950	.755	.700	.650
30	1.086	1.893	.524	.973	.423	.212
F-values						
Days	4.19*	14.76**	.76	31.87**	.62	5.88**
Day-night (diel)	8.46**	7.62**	5.36*	1.49	2.59	2.92
Depth	201.63**	18.31**	24.13**	106.64**	43.33**	132.38**
Days/Day-night	1.11	2.21	2.26	.32	3.29*	3.19
Days/Depth	.19	4.46**	.43	2.13	1.08	2.58*
Day-night/Depth	1.08	2.84*	.19	.58	.28	3.58*
Days/Day-night/Depth	.52	.19	.25	.66	.74	3.35**
Experiment 2: depths = 0, 2, 4, 6, 15, 30 m; times = 1800, 0000, 0600-1200 h						
Means:						
Overall	2.142	2.217	1.366	1.548	1.250	1.166
Times:						
1800	2.141	2.165	1.598	1.546	1.146	1.163
0000	2.225	2.348	1.595	1.514	1.336	1.107
0600-1200	2.061	2.138	.904	1.584	1.267	1.228
Depths:						
0	2.561	2.331	1.591	1.831	1.510	1.109
2	2.537	2.405	1.691	1.822	1.563	1.680
4	2.537	2.295	1.601	1.848	1.655	1.544
6	2.590	2.382	1.783	1.815	1.645	1.624
15	1.554	2.007	1.088	1.010	.764	.875
30	1.076	1.882	.440	.963	.361	.165
F-values						
Time of day	4.30*	8.68**	27.96**	.27	3.53	.75
Depth	139.11**	15.77**	23.07**	21.53**	57.70**	35.30**
Time/Depth	3.52*	1.67	2.00	.56	2.91*	1.41

*P = 0.05; **P = 0.01.

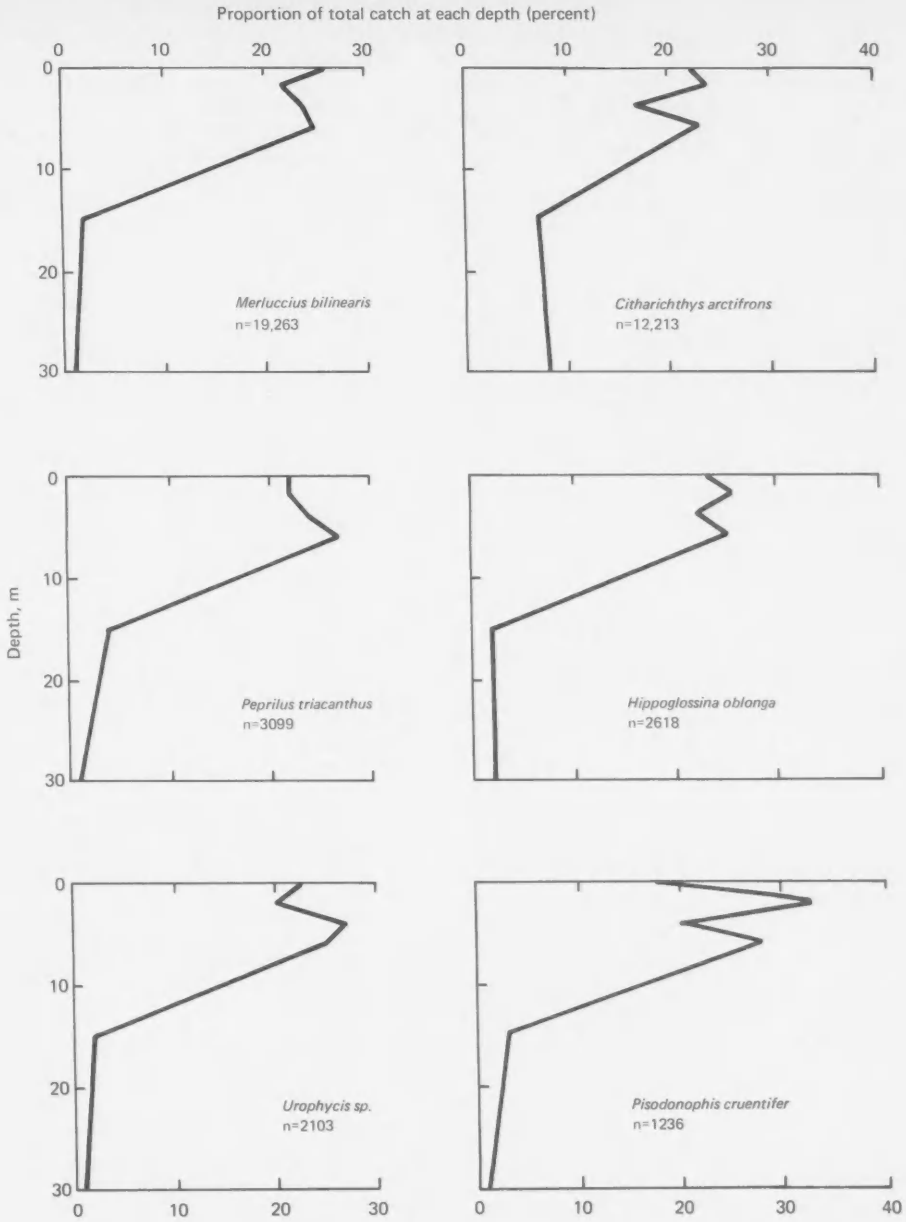

FIGURE 5.—Depth distribution of planktonic eggs of six species of fish collected during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

TABLE 5.—Stages of Atlantic whiting eggs taken in surface samples during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight. Roman numerals refer to batch numbers that were assigned to eggs.

Stage	Drogue station: / Time:	A 0600	B 0900	C 1200	D 1500	E 1800	F 2100	G 2400	H 0300	I 0600	J 0900	K 1200	L 1500	M 1800	N 2100	O 2400	P 0300	Q 0600	R 0900	S 1200	T 1500	U 1800	V 2100	W 2400	X 0300
Precell		III		1	49	26	6				IV	3	44	2					V	3	28	1			
2 cell					13	3	4						11	3							17				
4 cell					1		6						3								2				
8 cell							1														1	2			
16 cell		II			5	28	1														3	22			
Cell stage				5	28	7		4	5	2			15	53	5	22					11	22	4	1	
Early blastula		9	1		1	58	23	19	5	5				37	13	15	12	4	1		1	177	14	24	3
Blastodermal cap		7	1	1	1	32	161	19	5	5				16	121	29			1			63	183	28	94
Early germ ring		9	4	1	1	8	39	345	22	19					10	142	18	8				2	12	182	93
Germ ring ½ down		58	5	1	1		1	59	89	17	3					2	95	25	8	3			1	4	554
Germ ring ¾ down		46	21	2					283	15	5	1				1	54	42					1		198
Blastopore almost closed		28	31						176	25	16						3	11							9
Early middle		106	71	26					23	401	36	8					1	85	19	18	4				
Middle middle		54	164	51	19	1				40	380	23	3	1				1	107	12	25	2			
Late middle		1	37	137	44	9	1				42	79	29	2					7	155	67	19	1		
Early late				45	15	11					1	5	30	5						13	34	15	2		
Tail ⅝ around yolk	I	1		8	148	31	11	3				5	70	41	4						261	66	8	7	6
Tail ¾ around yolk		1		2	23	124	42	7					4	105	32	4	1				12	200	56	14	8
Tail ⅞ around yolk		8				10	170	47	4		1			4	98	13	6					6	160	99	35
Full circle		29	7				6	86	26	28					3	22	10	3					3	116	57
Tail 1⅛ around yolk		58	38	3				13	86	47	6	1			1		17	8	6					2	57
Abnormal late		6	2			20	14	21	4	5			1	2	1	30	14	16		2			2	9	12	7
Total		421	382	278	320	366	493	604	723	604	490	125	210	271	288	280	231	203	149	206	466	599	454	489	1,121

Kuntz and Radcliffe (1917) found that development in the laboratory required "not over" 43 h, but did not give temperature data.

During the cruise, all the eggs collected were spawned on 5 different days. Those spawned during the afternoon of the first sampling day (batch III) were the only ones sampled from spawning to hatching.

Batches of developing embryos spent roughly 3 h in each of the developmental stages listed in Table 5, except for the very early cell stages. From these data we derived a timetable of embryonic development (Table 6). Blastopore closure occurred about 12 h after spawning. Eggs were in middle stages of development, i.e., between blastopore closure and first appearance of the tail bud, for about 9 h. Hatching occurred about 15 h after tail bud formation.

The numbers of eggs in each batch are plotted according to developmental stage and time of day in Figure 6. Number of eggs taken varied widely from tow to tow; hence, we could not estimate mortality within any batch. In most tows, however, several obviously malformed late stages occurred in which embryos usually had ruptured yolks and shortened, rather wide tails. We assume that the condition of these embryos was not due to handling. These embryos, which composed up to 5.2% of an egg batch (Table 7), would probably not have survived to hatch.

The numbers of eggs taken at different times of day vary as batches are spawned and as they hatch (Figure 7). Because the eggs are spawned during only one period of the day (1500-1800 h), we would expect the maximum numbers of eggs to occur at

TABLE 6.—Timetable of development of Atlantic whiting eggs based on collections made during the vertical distribution study of ichthyoplankton in the Middle Bight, July 1974.

Time	Hours from spawning	Developmental stage
Day 1:		
1500	0	Precell
1800	3	Cell stage
2100	6	Early blastula
2400	9	Blastodermal cap
0300	12	Early germ ring
0600	15	Germ ring ½-¾ down
0900	18	Early middle
Day 2:		
1200	21	Middle middle
1500	24	Late middle
1800	27	Tail ⅝ around yolk
2100	30	Tail ¾ around yolk
2400	33	Tail ⅞ around yolk
0300	36	Full circle
0600	39	Tail 1⅛ around yolk—hatching
0900	42	Tail 1⅛ around yolk—hatching

about 1800 h; however, we found egg density to increase until 0300 h. The downward slope on the right side of the curves primarily reflects embryonic mortality, although hatching accounts for the decrease during the latest developmental stages. The fact that the egg batches reached their peak abundance later than expected probably reflects the influence of local currents on distribution of spawning adults and eggs.

TABLE 7.—Percentage of abnormal Atlantic whiting embryos in each spawning batch from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Batch	Total no. eggs	No. abnormal late stages	Minimum mortality (%)
I	153	8	5.2
II	2,012	64	3.2
III	3,224	64	2.0
IV	2,624	32	1.2
V	1,760	—	—

Determining the time and depth at which eggs were spawned provides information about adult spawning behavior. We have shown that newly spawned eggs appear in the afternoon and early evening. The depth at which spawning occurs can be estimated from knowing the depth at which the very early stage eggs were collected. Atlantic whiting eggs are planktonic, tending to rise toward the surface at a rate which, aside from turbulence of the water, depends on their specific gravity and that of the surrounding water. Estimating the rate of rise of the eggs in the water column enables us to calculate the depth at which

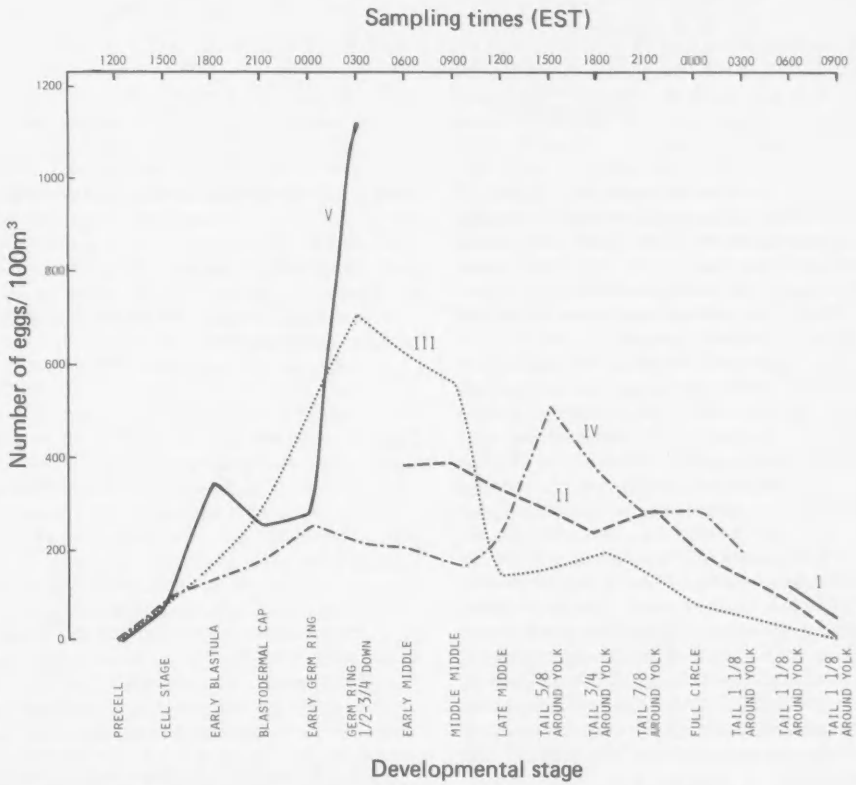

FIGURE 6.—Numbers of Atlantic whiting eggs in the five batches taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974, plotted by developmental stage and time of day.

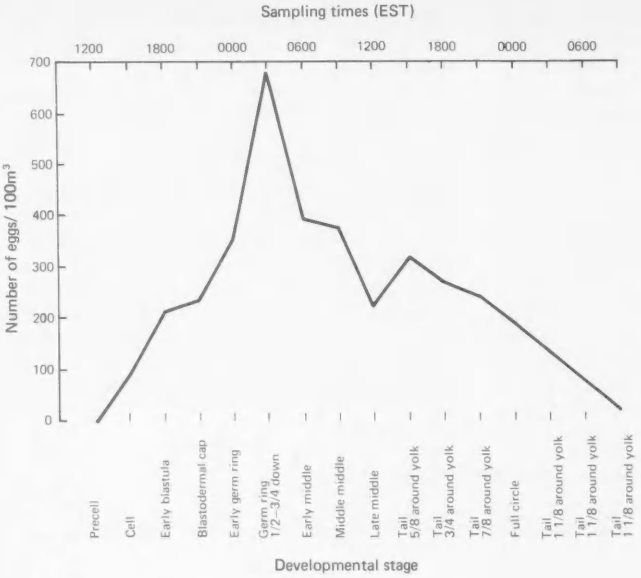

FIGURE 7.—Average number of Atlantic whiting eggs from spawning to hatching plotted by developmental stage and time of day, based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

the eggs were spawned. According to Stokes' law, Atlantic whiting eggs would have a rising velocity of 1.18 m/h or about 3.5 m during the 3-h interval between samples. Based on this and the fact that newly spawned eggs were taken primarily in the 0 and 4 m nets, the adults were spawning in the upper 10 m of the water column.

An overall mean of 30 Atlantic whiting larvae/ 100 m^3 was taken during the cruise. The numbers of larvae showed significant differences for all three primary factors (depth, time of day, and days) (Table 2). In general, the number of larvae caught increased with increasing depth (Figure 3). Significant numbers of larvae may have occurred below our 30 m sampling depth. A comparison of the numbers of larvae taken in the 15 and 30 m tows at various times of day (Figure 8) shows that more larvae were caught at 30 m during the day, while at night many more larvae were taken at 15 m. In general, more larvae were caught at night; however, on day 3 more were taken in the daytime. The larvae either avoided the nets more effectively in the daytime or more larvae migrated upward into the range of the nets at night.

Figure 9 shows the average lengths of larvae caught at 15 m and at 30 m. During the daytime, the 4.5 mm larvae were at 15 m while 6.5-9.2 mm larvae stayed at 30 m. At night, large larvae (6-9 mm) were at both 15 and 30 m, probably mixing with the small larvae, some of which may have sunk between 1800 and 0000 h, based on the decrease in mean length at 30 m and the increase in mean length at 15 m.

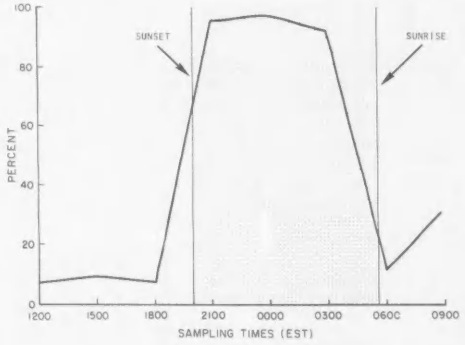

FIGURE 8.—Mean percentage of Atlantic whiting larvae at 15 m relative to larvae at 30 m by time of day from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

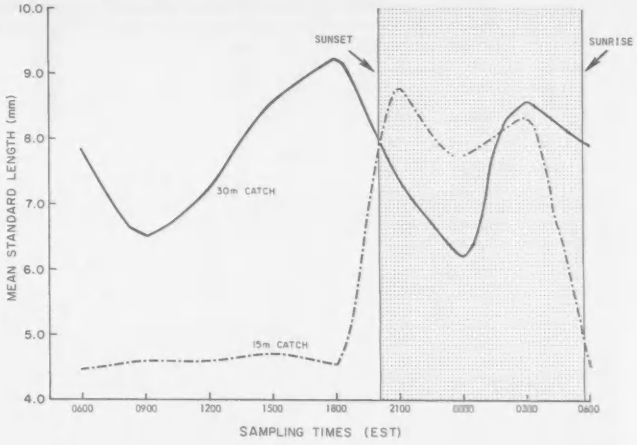

FIGURE 9.—Mean standard lengths (millimeters) of Atlantic whiting larvae taken at 15 and 30 m by time of day from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

We caught very few hatchlings (<3.0 mm [Kuntz and Radcliffe 1917]), as they appear to have been extruded from the 0.505 mm mesh net. Therefore, we could not detect a pulse in the numbers of very small larvae corresponding to the daily time of hatching or shortly thereafter. Significantly fewer larvae of all sizes were taken on day 3.

Gulf Stream Flounder

Gulf Stream flounder eggs have not been fully described in the literature, although Richardson and Joseph (1973) described eggs stripped from Gulf Stream flounder that were approaching spawning condition. The very small larvae are so similar to those of smallmouth flounder, *Etropus microstomus*, that the eggs also may be virtually indistinguishable from that species. In fact, eggs from our samples are identical to those described as smallmouth flounder eggs by Scherer and Bourne (1979), who did not provide adequate means of distinguishing the two species.

We have identified eggs from the plankton that we consider to be Gulf Stream and/or smallmouth flounder eggs based on egg and oil globule diameter and late embryonic characteristics. We assume that such eggs taken during this cruise are Gulf Stream flounder eggs for three reasons. First, Gulf Stream flounder occurs mainly at depths >46 m while smallmouth flounder is most common in water <27 m (Richardson and Joseph 1973); our samples were from an area where the water was 57 m deep. Second, smallmouth flounder larvae occur farther south than Gulf Stream flounder; our sampling location was in an area of peak Gulf Stream flounder abundance, but north of the area of maximum smallmouth flounder concentration (Smith et al. 1975). Finally, Gulf Stream flounder larvae occurred in markedly greater numbers in our samples than did smallmouth flounder larvae (19.7% as opposed to 1.5% of the total catch).

Gulf Stream flounder averaged 158 eggs/100 m^3 during the cruise. The catches were significantly different for all three primary factors (depth, time of day, and day) (Table 3). Fewer eggs were taken with increasing depth (Figure 5), though comparable numbers were taken at 15 and 30 m; more eggs were taken at night; and the total number of eggs increased with each day of sampling. More eggs were taken on each succeeding day at all depths except 30 m, where the number decreased with time.

Gulf Stream flounder eggs showed patterns of developmental stages that changed with both time and depth. Table 8 shows stages of eggs summed over all depths at each sampling time. The eggs were more difficult to separate into batches than Atlantic whiting eggs, but batches were defined in which eggs could be traced from spawning through hatching in succeeding samples. Usually three distinct groups of developmental stages were apparent at each sampling time. Precell stages were taken in the afternoon from 1500 to 2100 h. These eggs required about 3

TABLE 8.—Stages of Gulf Stream flounder eggs taken on day 1 during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974. Roman numerals refer to batch numbers that were assigned to the eggs.

Stage / Drogue station: / Time:	A 0600	B 0900	C 1200	D 1500	E 1800	F 2100	G 2400	H 0300
Precell	IV	1		25	19	5	V	2
2 cell				11	17	8	3	1
4 cell			2	2	15	15	1	
8 cell				2		4	12	
16 cell	2		3			11	1	
Cell stage	11	III 3			2	4	19	4
Early blastula	15	8	6	17	6	18	33	13
Blastodermal cap	86	84	43	17	38	18	41	32
Early germ ring	56	104	83	88	58	25	20	16
Germ ring ½ down	6	13	27	38	37	19	14	3
Germ ring ¾ down	7	9	4	12	17	21	10	3
Blastopore almost closed	9	II 3	6	7	10	8	20	
Early middle	22	15	5	4	4	19	38	8
Middle middle	16	13	8	6	6	6	19	20
Late middle	13	34	9	9	4	2	12	14
Early late	21	21	18	7	4	1	10	8
Tail ½ around yolk	5	11	1	7	4	1	1	2
Tail ⅝ around yolk	18	14	8	25	17	21	7	10
Tail ¾ around yolk	9	I 8	16	12	14	27	8	8
Tail ⅞ around yolk	11	6	7	15	15	16	32	10
Full circle	5	8	5	3	4	2	4	4
Total	312	355	251	307	291	251	305	158

full days to hatch; hatching occurred primarily in near-surface water beginning around 0900 h the morning of the fourth day after spawning.

Staging the eggs also revealed that they were stratified with depth, with early stages being taken in the deeper nets (Figure 10). Precell stages were taken primarily at 30 m, while eggs with several cell divisions and early blastula and blastodermal cap stages were taken mainly at 15 m. From 0900 to 1200 h the morning after spawning, early germ ring stages gradually shifted from 4 m to the surface. After 1200 h, the later stages were found at all depths sampled, but were concentrated at the surface and 4 m.

By using Stokes' law for calculating the rising velocity of the eggs, which have an average diameter of 0.70 mm, we estimated when the eggs were spawned and how old they were when sampled. If eggs were spawned on the bottom (57 m), they required 7 h to rise to 30 m and another 5.8 h to reach 15 m. As several precell and cell stage eggs appeared from 1500 to 1800 h in the 30 m net, the eggs were probably spawned between 0800 and 1100 h. Table 9 is a timetable for development of Gulf Stream flounder eggs based on the stages of eggs in Table 8 and on egg rising velocities calculated from Stokes' law.

The overlap between batches of the Gulf Stream flounder eggs as compared with the clearly defined batches of Atlantic whiting eggs may be related to two factors. First, the incubation time of Gulf Stream flounder is about twice that of Atlantic whiting eggs; therefore, eggs from twice as many batches are present in the plankton at once. Second, because Gulf Stream flounder spawns on the bottom, the eggs were subjected to turbulence and mixing by the time they were

TABLE 9.—Timetable of development of Gulf Stream flounder eggs based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Time	Hours from spawning	Developmental stage	Depth mainly taken (m)
Day 1:			
1500	7	Precell—cell stage	30
1800	10	Precell—cell stage	30
2100	13	Cell stage—early blastula	15
2400	16	Early blastula—blastodermal cap	15
0300	19	Blastodermal cap	15
0600	22	Blastodermal cap	15
0900	25	Early germ ring	4
1200	28	Early germ ring	4
Day 2:			
1500	31	Early germ ring	0-4
1800	34	Migrating germ ring	0-4
2100	37	Migrating germ ring	0-4
2400	40	Early middle	0-4
0300	43	Middle middle	0-4
0600	46	Middle middle	0-4
0900	49	Late middle	0-4
1200	52	Early late	0-4
Day 3:			
1500	55	Tail ⅝ around yolk	0-4
1800	58	Tail ⅝ around yolk	0-4
2100	61	Tail ¾ around yolk	0-4
2400	64	Tail ⅞ around yolk	0-4
0300	67	Tail ⅞ around yolk	0-4
0600	70	Tail ⅞ around yolk	0-4
0900	73	Full circle	0-4
1200+	76+	Hatching	0-4

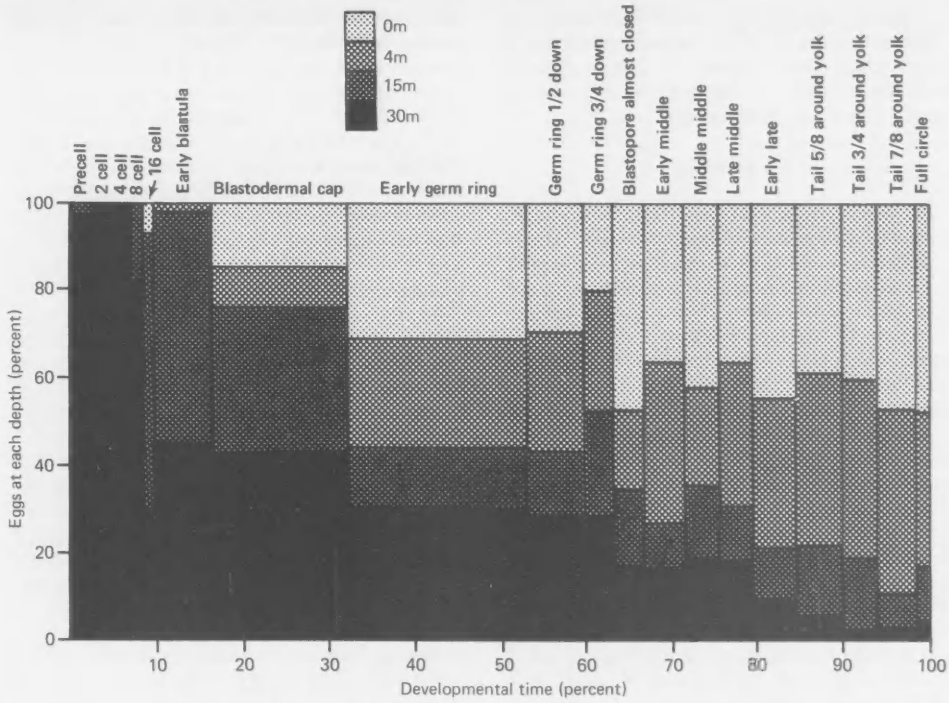

FIGURE 10.—Percentage of Gulf Stream flounder eggs at each depth plotted by age and stage based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

sampled, while Atlantic whiting eggs were collected from depths near where they were spawned.

An overall mean of 124 Gulf Stream flounder larvae/100 m^3 was taken during the cruise (Table 1). More larvae were taken at night than during the day and more were caught at 15 m than at the other depths sampled (Figure 3). The diel-depth interaction was significant in that Gulf Stream flounder, like fourspot flounder, were relatively more abundant at 0 and 4 m at night and at 15 and 30 m during the day, indicating a vertical migration upward at night (Table 2). Gulf Stream flounder larvae are concentrated in the thermocline during the day, but at least some move toward the surface at night.

From the second experiment, it appears that the movement toward the surface may occur in early evening because catches in the 2 m tow were high at 1800 h, while the 15 m tow took more larvae at other times (0000, 0600, and 1200 h). There was no significant difference in catches over the 3 d of the experiment, nor in the mean standard lengths, which ranged from 4.33 to 4.57 mm.

Smaller larvae were taken from 0 to 4 m during the day, while larger larvae were taken from 6 to 30 m (Table 10). At night, it seems that some of the larger larvae spread upward and were caught at

TABLE 10.—Mean standard lengths (millimeters) of Gulf Stream flounder larvae at six depths during day and night from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Depth (m)	Day			Night		
	Mean	SE	No.	Mean	SE	No.
0	3.31	0.267	12	4.10	0.278	114
2	3.55	.255	54	3.82	.370	55
4	4.03	.688	55	4.00	.217	185
6	5.93	2.188	27	4.04	.317	38
15	4.74	.172	328	5.22	.321	135
30	5.69	.414	177	4.40	.128	93

all depths; however, this result may be due to net avoidance by larger larvae near the surface in the daytime. These results are similar to those found for Atlantic whiting, in which larger larvae spread upward to 15 m at night.

Butterfish

An overall mean of 41 eggs/100 m^3 was caught during the cruise, making butterfish eggs third in abundance (Table 1). Fewer eggs were caught at the greatest sampling depths though the eggs at 4 m slightly outnumbered those at the surface (Table 4). In addition, more eggs were taken at night, which could reflect an evening spawning time. No significant differences in the number of eggs taken from day to day was evident.

An overall mean of 50 butterfish larvae/100 m^3 was taken during the cruise. There were no significant differences in numbers of larvae over the 3 d or during day as opposed to night (Table 2), indicating that we were probably sampling a uniform concentration of larvae throughout the experiment. In general, more larvae were taken at 15 m, but the diel-depth interaction indicated that the larvae were more abundant in the 0 and 4 m nets at night than during the day. This pattern is similar to that of Gulf Stream flounder and fourspot flounder indicating that some of the larvae that spend the day in the thermocline move toward the surface at night (Figure 3). The second experiment indicated that the 2 m catches were highest at 1800 h while the 15 m catches were high at all other times.

Fourspot Flounder

Fourspot flounder eggs ranked fourth in abundance, with a mean of 36 eggs/100 m^3 taken during the cruise (Table 1). Fewer eggs were taken at the greatest sampling depths though similar numbers were taken at 0 and 4 m and at 15 and 30 m (Figure 5, Table 4). No significant differences between day and night catches were evident.

An overall mean of 46 fourspot flounder larvae/100 m^3 was taken. The catches were significantly different for all three primary factors, i.e., more were caught at night than in the daytime, more were caught on day 3 than on the first 2 d, and the 15 m tow took more than the other three (Table 2). The interaction between days and depth was significant because on day 2 the surface and 4 m tows had high catches relative to the other days, while on day 3 the 15 and 30 m tows had high catches relative to the other days. Apparently the drogue, which was centered in the upper 10 m of the water column, did not experience the same drift during the experiment as the fourspot flounder larvae, which had their center of abundance in the thermocline at a depth of 15 m. The day-night depth interactions indicated migration by some larvae toward the surface at night since the 0 and 4 m tows had high catches at night while the 15 and 30 m tows had high catches during the day (see Figure 3).

Results of the second experiment show the same pattern in that more larvae were caught at night and the 15 m tow had high catches at all times. However, the 0, 2, 4, and 6 m tows had relatively higher catches at night than during either of the day periods.

These results indicate that fourspot flounder larvae occur mainly in the upper part of the thermocline where temperatures are above 10° C. Those larvae that move from 15 m during the day to near the surface at night, pass from 18° C water to 22° C water. The salinity also changes over this depth range from about 33.6‰ at 14 m to 32.8‰ at the surface.

Hakes

The species of hake (*Urophycis*) eggs and larvae in our samples could not be determined because of overlapping meristic characters and spawning seasons, so more than one species may be represented. An overall mean of 27 eggs/100 m^3 was taken, making hake eggs fifth in abundance. Slightly more eggs were taken at 4 m than at the surface (Figure 5), but otherwise egg numbers decreased with increasing depth (Table 4). No significant differences between day and night catches were evident, indicating that the daily spawning time was prolonged, or that we were possibly sampling more than one species with somewhat different spawning times. Egg concentration in the area of the drogue remained fairly constant. There were no significant differences among the 3 sampling days.

An overall mean of 146 larvae/100 m^3 was taken, making hakes the most abundant larvae caught (Table 1). In general, they were most abundant at 15 m (Table 2), but more were taken in the 0 and 4 m nets at night, and more in the 15 and 30 m nets during the day (Figure 3). During the second experiment, the time-depth interaction

was significant, indicating that during the three time periods examined, the larvae moved to shallower depths at night.

Snake Eel

Snake eel eggs ranked sixth in abundance, with an overall mean of 19 eggs/100 m^3. Fewer eggs were taken in the deeper tows, though slightly more eggs occurred at 4 m than at the surface (Figure 5). No significant difference between day and night egg catches was apparent (Table 4). However, at all depths except 15 m, more eggs usually were taken at night. At 15 m, more eggs were caught in the daytime. Significantly more eggs were caught on each succeeding day of the cruise.

The numbers of eggs in various stages taken during the cruise are shown in Table 11. Because the eggs were not stratified with depth, and because relatively few eggs were taken at each depth, we combined the eggs from the four depths sampled during the first experiment. The eggs are divided into seven batches that were spawned on the 3 d of sampling and the preceding 4 d. Where some ambiguity as to the boundary between older batches exists, replicate samples were staged to provide better definition of individual batches. At each sampling time, four groups of developmental stages were present. Spawning began at 2100 h each day, and was restricted to a relatively short period of time. Most eggs had hatched by 2100 h 4 d after being spawned. These data for development times have been used in a description of embryonic stages in this species (Naplin and Obenchain 1980).

The numbers of eggs in each batch are plotted according to developmental stage and time of day in Figure 11, from which the duration of each stage can be readily determined. For example, complete epiboly required about 12 h and took place from 0900 until 2100 h the day after the eggs were spawned. Table 12 is the corresponding complete developmental timetable for the snake eel. The regular fluctuations in egg number apparent in Figure 11 are even more clearly displayed in Figure 12, which depicts the total number of snake eel eggs over time. The fluctuations occurred on a 12-h cycle, and are possibly the result of tidal periodicity in spawning. As sampling progressed, the vessel gradually drifted into an area of more concentrated spawning, which was somewhat west of and closer to the 30-fathom (54.9 m) line

TABLE 11.—Stages of snake eel eggs taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974. Roman numerals refer to batch numbers that were assigned to the eggs.

Stage	Drogue station: Time:	A 0600	B 0900	C 1200	D 1500	E 1800	F 2100	G 2400	H 0300	I 0600	J 0900	K 1200	L 1500	M 1800	N 2100	O 2400	P 0300	Q 0600	R 0900	S 1200	T 1500	U 1800	V 2100	W 2400	X 0300
Precell or unfertilized							2								11								3		
2 cell							5								11								6		
Cell stage								1								2								5	
Early blastula							V	2							VI	7	2	19					VII	6	1
Blastodermal cap		16	2						8	12	2	1					14		27	2					64
Early germ ring		32		6	1						45	1									7	5			
Germ ring ½ down	IV			12	3							19	9							14	5	5			
Germ ring ¾ down				1	6	5							15	4								6	8		
Blastopore almost closed		7	3			7	3	1					3	20	3					1			15	35	1
Early and middle middle		2	4			2	21	14	8	11	2	1			30	19	6	11	8	1			1		22
Late middle		2		1	2		2		2	11	15			1			3	4	24	10					
Early late				6	2	2		1				11					2			7	5				
Tail ⅛ around yolk	III			1	1	1	10	2	4	2	1	2	5	10	10					1	13	16	29	6	3
Tail ¼ around yolk		2	1			1		5		2	5			4	8	10	4		1	1			8	27	14
Tail ⅞ around yolk	II	1							1	7		1					2	12	3	2					2
Full circle				1	2	6	1	1	3	1	1	1	2	2	1			3	3	1	2	2	3	2	6
Tail 1/8 around yolk		2				3	2			2			2	3	4	2				1	3	2	7	7	3
Tail 1¼ around yolk		1	1			1	1	1	1	2	1				4	2	3				1	1	7	8	12
Tail 1⅜ around yolk	I								2	2	1					2				3	1	1		1	1
Tail 1½ around yolk				1		1					1			1											2
Dead					1	1										1			2					2	
Total		30	44	29	16	32	47	28	29	52	74	37	36	45	81	46	36	50	70	43	37	30	87	97	131

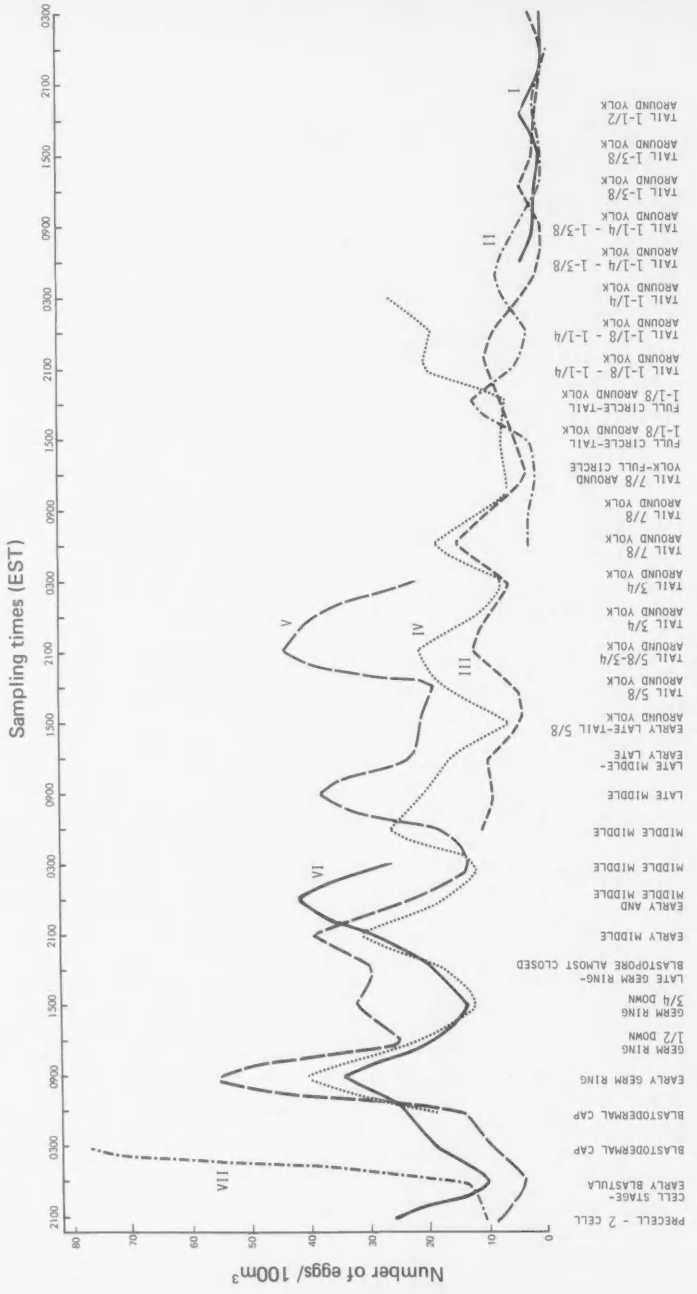

FIGURE 11.—Numbers of snake eel eggs in the seven batches taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974, plotted by developmental stage and time of day.

TABLE 12.—Timetable of development of snake eel eggs based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Time	Hours from spawning	Developmental stage
Day 1:		
2100	0	Precell—2 cell
2400	3	Cell stage—early blastula
0300	6	Blastodermal cap
0600	9	Blastodermal cap
0900	12	Early germ ring
1200	15	Germ ring ½ down
1500	18	Germ ring ¾ down
1800	21	Late germ ring—blastopore almost closed
Day 2:		
2100	24	Early middle
2400	27	Early and middle middle
0300	30	Middle middle
0600	33	Middle middle
0900	36	Late middle
1200	39	Late middle—early late
1500	42	Early late—tail ⅝ around yolk
1800	45	Tail ⅝ around yolk
Day 3:		
2100	48	Tail ⅝-¾ around yolk
2400	51	Tail ¾ around yolk
0300	54	Tail ¾ around yolk
0600	57	Tail ⅞ around yolk
0900	60	Tail ⅞ around yolk
1200	63	Tail ⅞ around yolk—full circle
1500	66	Full circle—tail 1⅛ around yolk
1800	69	Full circle—tail 1⅛ around yolk
Day 4:		
2100	72	Tail 1⅛-1¼ around yolk
2400	75	Tail 1⅛-1¼ around yolk
0300	78	Tail 1¼ around yolk
0600	81	Tail 1¼-1⅜ around yolk
0900	84	Tail 1¼-1⅜ around yolk
1200	87	Tail 1⅜ around yolk
1500	90	Tail 1⅜ around yolk
1800	93	Tail 1½ around yolk
2100	96	Hatching

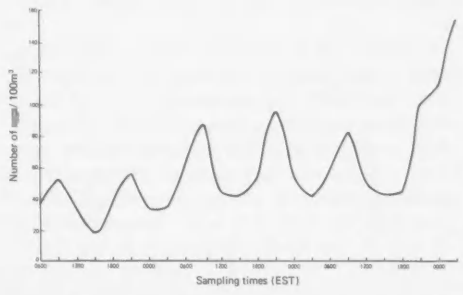

FIGURE 12.—Number of snake eel eggs during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974, plotted by time of day.

than the original sampling site. Because more eggs were taken each day, it was not possible to estimate the total size of any one batch.

A rough estimate of egg mortality within individual batches based on numbers of eggs at different times during their development and at corresponding points of the tidal cycle is approximately 0.5 to 0.6%/h, totaling 48 to 57.6% over the 96 h development time.

Applying Stokes' law to snake eel eggs results in an overall time of only 2.1 h required for eggs to rise from the bottom to the surface. The rapid rising velocity of the eggs is a result of their large diameter ($\bar{X}$ = 2.60 mm). Slightly more time would be required for eggs to rise to the surface if their density is somewhat greater immediately after spawning. In any case, if Stokes' law still holds for eggs of this size, it is inadequate for determining the depth of spawning for snake eel although from behavior of the adults it is likely to occur on or near the bottom.

Few snake eel larvae were caught during the cruise.

Frigate Mackerel

No frigate mackerel eggs were taken during the cruise. Due to nomenclatural confusion, the species of *Auxis* larvae in our collections cannot be determined. However, only one type of larva appears to be represented, and an overall mean of 54 larvae/100 m^3 was caught during the cruise. There were highly significant differences in days, diel, and depth factors (Table 2), indicating that we were not sampling a uniformly distributed population during the experiments. The larvae were more abundant at night than during the day, and more were caught on the second day than on the first or third. Larvae were most abundant overall in the 4 m tow, and more were taken at the surface during day than at night. Catches at 15 and 30 m were so small in both day and night tows that contamination of the nets in shallower water as they passed through the water column could account for them (Figure 3). In the second experiment, the 2 m tow caught most fish at 1800 h, while the 6 m tow caught more at other times. Thus *Auxis* larvae were mostly in the upper 6 m of the water column above the thermocline and were found closer to the surface during the evening.

Smallmouth Flounder

Smallmouth flounder eggs have not been described. Based on the similarity of the early larvae, however, it is likely that they closely resemble Gulf Stream flounder eggs. In view of

the relative proportions of larvae of the two species taken during the cruise, eggs with characteristics of smallmouth flounder and Gulf Stream flounder were assumed to be of the latter species.

An overall mean of 9.1 smallmouth flounder larvae/100 m^3 was taken during the cruise. In general, the 15 m tow caught most of the larvae; however, more larvae were taken at 15 and 30 m in the daytime, while more were caught at 0 and 4 m at night (Figure 3). The larvae moved toward the surface at night and were also more abundant at all depths at night. More larvae were taken on each succeeding day of the experiment (Table 2).

We found little difference in mean length during day tows at all depths, and although the larvae caught at night at 30 m were larger than those caught at other depths, only two were taken (Table 13). The mean lengths of the larvae taken each day remained virtually constant from 3.58 to 3.61 mm. Evidently the drogue gradually drifted into an area of higher larval concentration, resulting in the increasing number of larvae taken each succeeding day.

TABLE 13.—Mean standard lengths (millimeters) of smallmouth flounder larvae at six depths during day and night from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Depth (m)	Day			Night		
	Mean	SE	No.	Mean	SE	No.
0	—	—	—	3.65	0.102	87
2	3.73	0.515	38	3.41	.410	52
4	4.14	.390	15	3.63	.078	135
6	4.48	.765	8	3.60	.350	40
15	3.42	.098	200	4.06	.298	78
30	4.13	.932	13	5.30	.300	2

DISCUSSION

The two major techniques applied to the egg data, i.e., analyses of variance of egg numbers based on a factorial experimental design and staging the eggs, tend to complement each other. The former technique is used to point out significant variation in the data that may be clarified and elaborated by staging selected egg samples. For example, significant differences in egg number at various times of day revealed by factorial analysis can be accounted for by the daily spawning and hatching cycles revealed by staging the eggs. In our experiments, analysis of variance demonstrated significant changes in egg numbers over four sampling depths, over 3 d, and in the daytime and at night. Egg staging provided us with developmental timetables, and time of day and depth of spawning and hatching. Spawning and developmental characteristics of the three species whose eggs were staged are summarized in Table 14. Atlantic whiting and snake eel eggs were distributed homogeneously by stage over all depths sampled, whereas Gulf Stream flounder eggs were stratified by stage to some extent. Stage stratification of Gulf Stream flounder eggs indicated that spawning probably occurred on the bottom, and rising velocity calculations for these eggs support that conclusion. The rising velocity for Atlantic whiting eggs narrowed the possible spawning depth to the upper 10 m of the water. Fluctuations in egg numbers that appeared to be tide induced could indicate that the bottom-dwelling snake eel spawns on the bottom during a particular time of the tidal current cycle.

In a study of haddock eggs, Walford (1938) found that the eggs were spawned on the bottom and had a tendency to rise. Because egg stages were homogeneously distributed with respect to depth, he concluded that the eggs could adjust their specific gravity within limits to match that of the ambient water. Most planktonic eggs probably possess some capacity to adjust their densities (Walford 1938). However, because a definite age stratification with depth appeared for the Gulf Stream flounder eggs, we can conclude that in this case the eggs rise in the water column more rapidly than they adjust their density to the ambient water.

Spawning and hatching times for the three species were staggered throughout the day, with no two species having similar schedules. Atlantic whiting and snake eel spawned in the afternoon and evening, and while Atlantic whiting eggs hatched in the morning, snake eel eggs hatched at about the same time of day they were spawned.

TABLE 14.—Summary of local characteristics of distribution of spawning and development determined by staging eggs of Atlantic whiting, Gulf Stream flounder, and snake eel, based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Characteristic	Atlantic whiting	Gulf Stream flounder	Snake eel
Stage vs. depth	Same stage at all depths	Earliest stages deepest	Same stage at all depths
Spawning depth	Upper 10 m	Bottom (57 m)	Bottom
Spawning time, h	1500-1800	0800-1100	2100
Hatching time, h	0300-0800	1200-1500	1500-2100
Incubation time	1.5 d (39 h)	3 d (72 h)	4 d (96 h)
No. stages/samples	Usually 2	Usually 3	4

Gulf Stream flounder spawned in the morning and the eggs hatched around noon. The progression from precell to hatching stages in all of these species allowed construction of detailed developmental timetables. Ahlstrom (1943) found spawning to occur during only a few hours of the day, and that plankton samples contained discrete batches of eggs spawned on different days. He also determined developmental times from this information. Ferraro (1980) reported on daily spawning times of a number of species. All fish investigated spawn during limited times of day, mainly at some time between noon and midnight.

For species that spawn on a regular diel basis, the number of predominant stages at any time about equals the number of days the eggs require to hatch (Table 14). Therefore, longer incubation times mean that more days of spawning are represented at any one time, making the separation of eggs into discrete spawning batches more difficult. Atlantic whiting eggs, with a short incubation time and spawned in the upper 10 m of water, were readily separated into discrete batches. Theoretically, snake eel eggs with a development time of 96 h would be more difficult to separate into batches than Gulf Stream flounder eggs with a development time of only 72 h. This was not the case, probably because of the depth stratification of the Gulf Stream flounder eggs and their longer daily spawning period compared with the homogeneous depth distribution of snake eel eggs and their very short daily spawning period.

Among the eight most abundant types of larvae collected during this study, all were more abundant closer to the sea surface at night. Two general patterns were seen: bluefish and frigate mackerel larvae were mostly above the thermocline (most abundant at 6 m) and some migrated to the surface at night; the other six species were most abundant below the thermocline at 15 m during the day but some larvae of each species migrated to waters above the thermocline at night. Within these two patterns, specific variations occurred. No two species showed the same combination of significant F-values for the factors tested and their interactions. We remained in a body of water where factors affecting larval abundance were so constant for three of the species that no significant differences were seen in the catches over the 3-d study. The two species most closely associated with the surface (bluefish and frigate mackerel) showed the greatest fluctuations in abundance over the 3 d, indicating that in following the drogue, we moved to areas where variation in factors affected larval abundance occurred. In such areas where water movement varies considerably with depth, a drogue can be expected to track only uniform patches of those organisms whose depth ranges are similar to that of the drogue. Four species were collected in significantly larger numbers at night than during the day. This may have resulted from increased avoidance by larvae during daylight. However, significantly more Atlantic whiting larvae were taken during day than at night. Some of these differences may thus reflect differences in vertical distribution on a diel cycle. If the larvae were more concentrated during day than at night at one or more of the levels sampled, they would appear more abundant during the day, although their overall abundance in the water column would not actually be different. Significant portions of the larval population of species that were abundant in our deeper nets may have occurred below the depths we sampled.

This study, as have others (e.g., Miller et al. 1963), points out the necessity of sampling the entire water column, at least over continental shelves, during ichthyoplankton surveys. This is accomplished in the many recent surveys which employ oblique or vertical plankton tows. In other sampling designs significant portions of the populations can be either undersampled or oversampled depending on their depth distribution and the time of day of sampling. The implications of this study regarding effects of time of day on numbers of fish eggs in the water column due to diel spawning and embryonic developmental cycles need to be considered in analyzing results of ichthyoplankton surveys.

ACKNOWLEDGMENTS

We extend our appreciation to the many members of the staff of Sandy Hook Laboratory for their help at sea and in the laboratory in gathering and processing the samples on which this paper is based. Special thanks are due to W. G. Smith and Jack Colton who reviewed drafts of the manuscript.

LITERATURE CITED

AHLSTROM, E. H.
1943. Studies on the Pacific pilchard or sardine (*Sardinops*

caerulea). 4. Influence of temperature on the rate of development of pilchard eggs in nature. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 23, 26 p.

1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

BOWMAN, M. J., AND L. D. WUNDERLICH.

1977. Hydrographic properties. MESA New York Bight Atlas Monogr. 1, 78 p. N.Y. Sea Grant Inst., Albany.

BREDER, M., AND D. E. ROSEN.

1966. Modes of reproduction in fishes. Am. Mus. Nat. Hist. Press, Garden City, N.Y., 941 p.

BRIDGER, J. P.

1956. On day and night variation in catches of fish larvae. J. Cons. 22:42-57.

DEUEL, D. G., J. R. CLARK, AND A. J. MANSUETI.

1966. Description of embryonic and early larval stages of bluefish, *Pomatomus saltatrix*. Trans. Am. Fish. Soc. 95:264-271.

DIXON, W. J. (editor).

1973. BMD biomedical computer programs. 3d ed. Univ. Calif. Press, 773 p.

ENGLISH, T.

1961. An inquiry into distributions of planktonic fish eggs in a restricted area of Puget Sound. Ph.D. Thesis, Univ. Washington, Seattle, 227 p.

FERRARO, S. P.

1980. Daily time of spawning of 12 fishes in the Peconic Bays, New York. Fish. Bull., U.S. 78:455-464.

KANOH, Y.

1954. On the buoyancy of the egg of Alaska pollack, *Theragra chalcogramma*. Jpn. J. Ichthyol. 3:238-246.

KENDALL, A. W., JR., AND L. A. WALFORD.

1979. Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. Fish. Bull., U.S. 77:213-227.

KUNTZ, A., AND L. RADCLIFFE.

1917. Notes on the embryology and larval development of twelve teleostean fishes. Bull. U.S. Bur. Fish. 35:87-134.

LEIS, J. M.

1977. Development of the eggs and larvae of the slender mola, *Ranzania laevis* (Pisces, Molidae). Bull. Mar. Sci. 27:448-466.

MILLER, D., J. B. COLTON, JR., AND R. R. MARAK.

1963. A study of the vertical distribution of larval haddock. J. Cons. 28:37-49.

NAPLIN, N. A., AND C. L. OBENCHAIN.

1980. A description of eggs and larvae of the snake eel, *Pisodonophis cruentifer* (Ophichthidae). Bull. Mar. Sci. 30:413-423.

RICHARDSON, S. L., AND E. B. JOSEPH.

1973. Larvae and young of western north Atlantic bothid flatfishes *Etropus microstomus* and *Citharichthys arctifrons* in the Chesapeake Bight. Fish. Bull., U.S. 71: 735-767.

RUSSELL, F. S.

1926. The vertical distribution of marine macroplankton. III. Diurnal observations on the pelagic young of teleostean fishes in the Plymouth area. J. Mar. Biol. Assoc. U.K. 14:387-414.

SALEKHOVA, L. P.

1959. O razvittiilufarya (*Pomatomus saltatrix* Linne) (On the development of the bluefish (*Pomatomus saltatrix* Linne)). [In Russ.] Tr. Sevastop. Biol. Stn. 11:182-188. (Transl. by R. H. Backus, 1962, 13 p., available Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.)

SCHERER, M. D., AND D. W. BOURNE.

1979. Eggs and early larvae of smallmouth flounder, *Etropus microstomus*. Fish. Bull., U.S. 77:708-712.

SELIVERSTOV, A. S.

1974. Vertical migrations of larvae of the Atlanto-Scandian herring (*Clupea harengus* L.). *In* J. H. S. Blaxter (editor), The early life history of fish, p. 253-262. Springer-Verlag, N.Y.

SMITH, W. G., J. D. SIBUNKA, AND A. WELLS.

1975. Seasonal distributions of larval flatfishes (Pleuronectiformes) on the continental shelf between Cape Cod, Massachusetts, and Cape Lookout, North Carolina, 1965-66. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-691, 68 p.

1978. Diel movements of larval yellowtail flounder, *Limanda ferruginea*, determined from discrete depth sampling. Fish. Bull., U.S. 76:167-178.

WALFORD, L. A.

1938. Effects of currents on distribution and survival of the eggs and larvae of the haddock (*Melanogrammus aeglefinus*) on Georges Bank. U.S. Bur. Fish., Bull. 49:1-73.

WRIGHT, W. R., AND C. E. PARKER.

1976. A volumetric temperature/salinity census for the Middle Atlantic Bight. Limnol. Oceanogr. 21:563-571.

ZARET, T. M., AND J. S. SUFFERN.

1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. 21:804-813.

RESPONSES OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE TO PREDATION BY A BITING PLANKTIVORE, *AMPHIPRION PERCULA*

P. W. WEBB[1]

ABSTRACT

Responses of northern anchovy larvae, ranging from 0.29 to 1.2 cm total length, to attacks by a biting planktivore, the clown fish, were recorded on video tape. Schlieren optics were used to simultaneously view an opaque predator and transparent prey. All fish were reared, and experiments performed, at 20° C. The percentage of larvae responding to attacks increased from about 9% for 0.29 cm larvae to 80% for 1.2 cm larvae. Of these larvae responding to attack, 26 ± 10% attempted to escape too late and were caught. This proportion was not related to larval size. The direction of larval escape paths to the initial orientation of the body was not related to larval size, but escape distances traveled and mean escape speeds increased with size from 1.0 cm and 4.0 cm/s respectively for larvae 0.29 cm total length to 3.5 cm and 8.2 cm/s in larvae 1.2 cm total length. Larval performance was not maximal except during rare chases which occurred in 7% of attacks by the predator.

Escape maneuvers in vertebrates are initiated by the magnifying retinal image of an approaching object, called the looming effect, and calculated as the rate of change of the angle subtended by the predator as seen by the prey. In the present study, apparent looming thresholds for larval avoidance responses were calculated at the start of the response, and differ from the true response because there must be a finite time difference between the stimulus exceeding the response threshold and the motor response itself (response latency). Maximum likelihood mean apparent looming thresholds were calculated for log-transformed data, assuming nonresponding prey had apparent looming thresholds greater than the maximum actually observed. These mean apparent looming thresholds decreased with larval length from approximately 32 rads/s at 0.29 cm to 1.7 rads/s at 1.2 cm. The most important feature of the larval avoidance response was that an escape attempt should be made appropriately timed to an attack.

The method could be used to examine larval fish responses in other interactions where predation events take place over a small distance. Examples are attacks by biting juvenile and adult fish, and other planktonic invertebrate predators. Effects of larval density and alternate prey species could also be evaluated.

Predation and starvation are believed to be the dominant factors contributing to the extensive mortality of fish eggs and larvae (Blaxter 1969; Hunter 1977, in press; Hunter and Kimbrell 1981). Following Hjort's critical period concept concerned with the importance of first-feeding success to larval survival (Hjort 1914), most attention has concentrated on feeding behavior and food consumption (e.g., Hunter 1972, in press; Arthur 1976; Lasker 1978). Fish eggs and larvae are also extremely vulnerable to a wide variety of fish and invertebrate predators. A few experimental studies have determined feeding rates for invertebrate predators on eggs and larvae in the laboratory (Lillelund and Lasker 1971; Theilacker and Lasker 1974; von Westernhagen and Rosenthal 1976) and rates of egg cannibalism by fish in the field (Hunter and Kimbrell 1981). I know of no studies that have examined responses of larvae to a fish predator.

Northern anchovy, *Engraulis mordax*, larvae are exposed to a wide range of juveniles and adults of fish and consequently to a range of feeding habits on a continuum from filter-feeding to biting (e.g., Leong and O'Connell 1969). The purpose of the experiment described here was to develop a method to study responses of northern anchovy larvae to attacks by fish, and to determine how avoidance responses and larval vulnerability to capture change during early development. A biting fish planktivore was used as a predator in an attempt to complement studies relating to filter-feeding predators, often crudely simulated by towed plankton nets (e.g., Webb and Corolla 1981).

METHODS

Northern anchovy larvae were reared from eggs

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, Calif.; permanent address: The University of Michigan, School of Natural Resources, Ann Arbor, MI 48109.

Manuscript accepted: June 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

as described by Hunter (1976). Eggs were spawned from five groups of adults taken from laboratory stocks on five occasions during spring 1980 (Table 1.) Eggs were transferred to noncirculated filtered sea water in 400 l black fiber glass tanks. Food for larvae was the dinoflagellate *Gymnodinium splendens* for 2- to 5-d-old larvae, and the rotifer *Brachionus plicatilis* for older larvae. Water temperature was maintained at 20° C. Larvae were held under constant illumination of 2,000 lx at the water surface, provided by standard room fluorescent lights.

Observations were made on predation of eggs and 10 groups of larvae of different total lengths, ranging from 0.29 to 1.2 cm (Table 1). Lengths were based on measurements of a subsample from each group at the time they were used for experiments. Observations were concentrated on early larvae because this is the period of greatest morphogenesis (O'Connell 1981) and maturation of response systems (Kimmel 1972; Webb and Corolla 1981).

TABLE 1.—Total length of subsample ($\bar{X} \pm 2$ SE; $N = 10$) of northern anchovy larvae populations used in predation experiments with a model predator, the clown fish. Data are also given on spawnings.

Total length at test (cm)	Group	Date spawned (1980)	Date tested
Eggs[1]	C	13 Mar.	13 Mar.
Larvae 0.287 ± 0.015	C	13 Mar.	14 Mar.
.322 ± 0.008	E	4 Apr.	5 Apr.
.391 ± 0.020	E	4 Apr.	6 Apr.
.399 ± 0.010	E	4 Apr.	7 Apr.
.417 ± 0.011	E	4 Apr.	8 Apr.
.421 ± 0.011	B	28 Feb.	4 Mar.
.626 ± 0.050	B	28 Feb.	12 Mar.
.867 ± 0.053	D	27 Mar.	14 Apr.
.953 ± 0.090	A	7 Feb.	29 Feb.
1.166 ± 0.095	A	7 Feb.	18 Mar.

[1]Eggs were 0.135 ± 0.005 cm long × 0.069 ± 0.003 cm wide.

Attempts to obtain natural predators of uniform and suitable size were not successful. Therefore a mimic for biting predators was used. This model was the clown fish, *Amphiprion percula*, cultured from eggs. The fish were held in 40 l polypropylene tanks at 20° C and under constant illumination. The fish were fed daily on a diet of Tetramin[2] and northern anchovy eggs and larvae. The predator was readily available at uniform sizes throughout the duration of the experiment. The clown fish were 4.4 ± 0.2 cm total length (TL) and mass was 1.58 ± 0.17 g. The maximum depth was 1.8 ± 0.2 cm, and maximum width 0.6 ± 0.1 cm, both located 1.3 ± 0.1 cm from the nose (data are $\bar{X} \pm 2$ SE; $N = 10$).

Interactions between the model predator and northern anchovy eggs and larvae were observed using schlieren optics (Holder and North 1963). Briefly, a vertical collimated light beam was produced by a high intensity monochromatic point source at the focus of a concave mirror (focal length 140 cm) attached to the ceiling. A second mirror, with the same focal length, was located at the floor and focused the light on a black spot on a glass plate.

The observation arena was a cylindrical tank, located in the light beam. It was 35 cm in diameter and 10 cm deep and had a plate-glass bottom. The tank contained a central cylinder, 26.5 cm in diameter and 5 cm deep, which supported a circular plate-glass lid. The lid and the bottom were parallel to each other and normal to the light beam. Discontinuities in refractive index (i.e., larvae in the water) deflected the light from the focus spot on the glass plate, and were seen as bright objects against a dark background. Opaque objects (i.e., the predator) were seen as black silhouettes.

The clown fish were starved for 5 d to ensure uniform high motivation. This was necessary because northern anchovy larvae grow rapidly and loss of a day required starting new batches, particularly for young larvae. Individual clown fish were placed in the observation arena and left for 24 h. After this period, up to 100 northern anchovy eggs and larvae were introduced through a side port in the central cylinder. After 10 to 30 min, the predator began feeding on the prey distributed through the tank. The reason for the delay in the onset of feeding is not known. Behavior was recorded on video tape. Experiments were performed at 20° C.

The video tape was manually advanced to analyze images frame by frame (framing rate = 60 Hz). The following observations were made: the number of attacks by clown fish, escape attempts by prey, escape success of the prey, catch success of the predator, and the number of predator errors. The prey escape angle, distance traveled, and mean speed during an escape attempt were measured.

Animals from a wide range of taxa, including fish, show avoidance responses to approaching, presumably threatening objects (see Gibson 1980). The image of such an object on the retina expands rapidly and this magnification in time is called the "looming effect." It is measured as the rate of

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

change of the angle, α, subtended by the approaching object measured at the prey's eye (Dill 1974a, b). The looming effect is greater as the speed of an approaching object increases, as the object gets closer, and for larger objects. The threshold was calculated at the start of an escape attempt by the larvae, after Dill (1974a),

$$\frac{d\alpha}{dt} = \frac{4\,U\,S_h}{4(D+d)^2 + {S_h}^2} \quad (1)$$

where U = predator speed at the time of the prey response,
S_h = predator shape; mean of maximum depth and width of the clown fish,
D = distance between the predator's nose and the prey when the prey responded,
d = posterior distance of the predator's maximum depth and width from its nose.

Here, $d\alpha/dt$ at the start of the response by the larvae is called the apparent looming threshold (ALT). This is because the true threshold must occur prior to the observed motor response because there is a finite delay in the nervous system between receipt of the stimulus and the start of the motor response. The value of this response latency, or reaction time, is unknown for northern anchovy larvae.

RESULTS

Clown fish fed discontinuously on eggs and larvae, feeding intensely on prey in one location and then swimming around the tank before feeding again. Thus the clown fish did not attack prey as encountered, and often ignored nearest prey between feeding bouts. The clown fish were continuously active, swimming mainly by paddling movements of the pectoral fins supplemented with caudal fin beats. The mean speed was 3.2 ± 0.5 cm/s ($\bar{X} \pm 2$ SE; $N = 100$; range 0.5 to 9.1 cm/s).

Attacks were made on individual larva. Orientation by the clown fish prior to a strike could not be distinguished with confidence from normal swimming. Prey that did not attempt to escape were always caught, with the exception of eggs and the smallest larvae tested. Thus 12% of strikes on eggs and 3% of strikes on nonresponding 0.29 cm larvae were not successful. Predator failures are presumed due to predator error, which has been reported as 8% for largemouth bass, *Micropterus salmoides*, (Nyberg 1971) and 34% for chain pickerel, *Esox niger* (Rand and Lauder 1981). Larvae that made an avoidance response to an attack by clown fish were rarely pursued because clown fish usually attacked another larva. Eight chases were observed in 113 escape attempts by northern anchovy larvae. One escape each was observed for larvae in the 0.626 and 1.166 cm TL groups and two in each of the 0.399, 0.867, and 0.953 cm groups.

Larval responses to attacks by clown fish were characteristic startle responses, followed by a short period of sprint swimming. The startle response consisted of a C-start form of a fast start and a turn (Eaton et al. 1977). The sprint was a period of swimming at constant speed for <1 s (see Hoar and Randall (1978) for definitions). Together, these two components constitute a swimming burst (Webb and Corolla 1981).

The proportion of larvae responding to attacks increased with size, from approximately 9% for 0.29 cm larvae to 80% for 1.2 cm larvae (Figure 1A). The proportion of larvae escaping an attack similarly increased with size, but at a lower rate than the proportion making an escape attempt (Figure 1B). This was because $26 \pm 10\%$ ($N = 10$ groups of larvae) of larvae showing an escape response were eaten anyway, before a chase began. These larvae were defined as attempting to escape too late. This proportion of escaping larvae caught

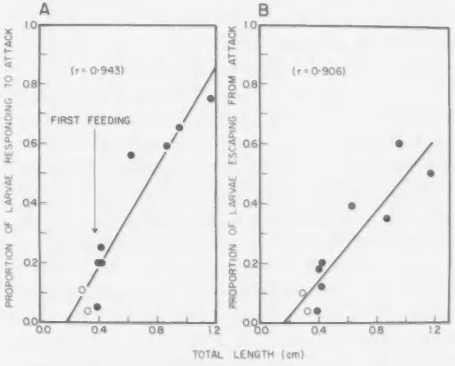

FIGURE 1.—Relationships between (A) the proportion of northern anchovy larvae responding to an attack by clown fish and (B) the proportion escaping an attack, both as functions of the total length. Circles are for prefeeding yolk-sac larvae.

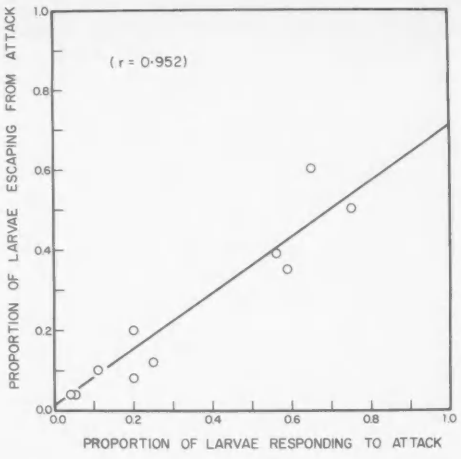

FIGURE 2.—The relationship between the proportion of northern anchovy larvae responding to an attack and the proportion escaping an attack by clown fish.

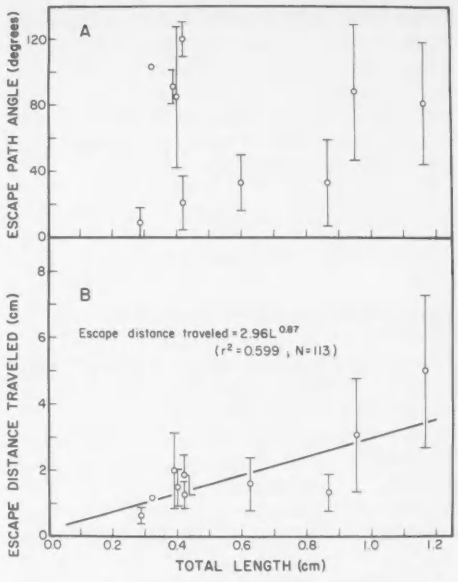

FIGURE 3.—The relationship between (A) the angle of the prey escape path to the predator's strike path and (B) escape distance traveled both as functions of total length of northern anchovy larvae attacked by clown fish. Vertical bars show ±2 SE.

by the clown fish was not correlated with larval size.

The proportion of larvae attempting to escape was therefore related to the proportion escaping (Figure 2). Using functional regression analysis (see Ricker 1979), the relationship was found to be linear, and gave a value of 30% of larvae attempting to escape being captured. This is within the expected range obtained from observations on each group of larvae.

The startle response included a turn. The angle of the prey escape path relative to the predator strike path showed no particular relationship with larval length (Figure 3A), but this was primarily due to the large angles measured for the 0.391, 0.399, and 0.421 cm larvae. Without these data, the escape angle would have increased with larval length, implying larger larvae were better at avoiding the predator's strike path. However, larvae in the three length classes with large angles did not differ from others in any obvious way, and therefore the data cannot be rejected.

However, the distance traveled in an escape swimming burst increased with larval total length (Figure 3B). Using regression analysis (type II) the relationship was best described by a power function, but r^2 values were relatively low. Mean escape speeds in an escape swimming burst also increased with larval size (Figure 4). These speeds were normally about half the mean burst speeds obtained in a forced swimming burst (Webb and Corolla 1981), but escape speeds comparable with the forced maximum were seen during chases.

Analysis of ALT's for larval escape responses is somewhat complex. These ALT's were assumed to be distributed in the population like any other character. However, not all larvae responded. Since nonrespondants were eaten before responding they were assumed to have higher ALT's than larvae showing escape responses. Therefore, the true distribution of ALT's in the population is not known as values above some observed level are missing. Such a population is said to be censored, and since values are missing from one end of the distribution only, it is said to be singly censored. Cohen (1961) has described methods to calculate the maximum likelihood mean and variance of such censored samples. However, before this can be done, the nature of the ALT distribution must be considered.

The nature of the distribution of ALT's in the population was evaluated using probit analysis, developed to examine related problems in toxicology (Sprague 1969). ALT values were ranked and

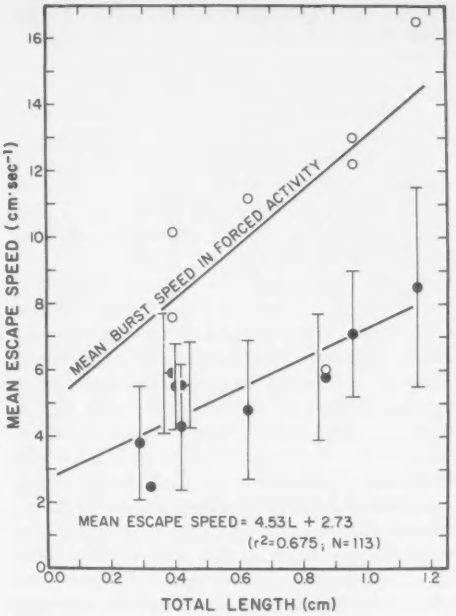

FIGURE 4.—The relationship (dots) between mean escape speed and total length of northern anchovy larvae attacked by clown fish. Vertical bars are ±2 SE. Circles show mean escape speeds during chases. The line for mean burst speeds was taken from Webb and Corolla (1981).

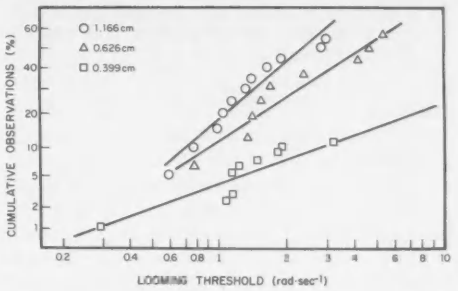

FIGURE 5.—Representative relationships between cumulative number of startle responses, expressed as percentages of total attacks (probit scale) and the logarithm of ALT's for northern anchovy larvae of three different total lengths.

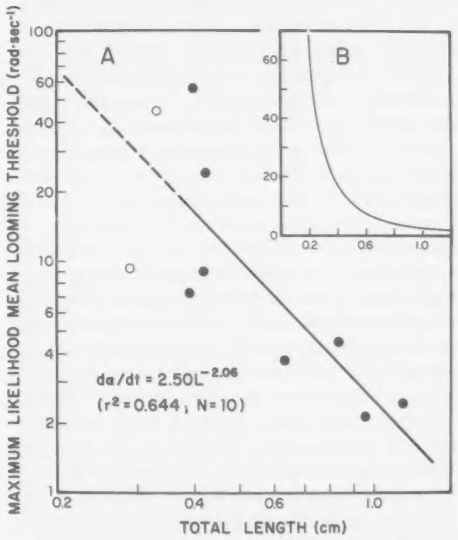

FIGURE 6.—The relationship between the maximum likelihood mean ALT and total length of northern anchovy larvae attacked by clown fish. The relationship is shown for logarithmic coordinates in (A) and for arithmetic coordinates in the inset (B). Circles are for prefeeding yolk-sac larvae.

the cumulative percentage of observations was plotted on a probit scale against these values. A logarithmic transformation of ALT values linearized the relationship to the greatest extent (Figure 5) implying ALT's were log-normally distributed in the population. Some curvature remained after this transformation, probably due to decision errors (Treisman 1975) and individual variability in response latencies. Thus ALT values were assumed to be log-normally distributed in the larval populations sampled, and maximum likelihood means and variances were calculated for a type I singly censored sample (Table 2) as described by Cohen (1961). Resulting mean ALT's are shown as a function of total length in Figure 6.

The most important result from this analysis was that ALT's decreased rapidly with increasing size, and hence development, tending towards a plateau for larger larvae and presumably for adults. The relationship was best described by a power function with a negative exponent (see Figure 6) but such a description should be treated with caution. This is because the ALT distributions were severely censored, with a resulting large variance about each mean. In addition, the residual curvature in the transformed data could influence mean ALT values, but this would not alter the general shape of the inverse relationship between ALT's and larval size.

TABLE 2.—Parameters used in the calculation of maximum likelihood values of the population mean $d\alpha/dt$ ($\tilde{\mu}$) and variance ($\tilde{\sigma}^2$) for northern anchovy larvae responses to clown fish predators, using the method of Cohen (1961). Logarithm-transformed data for $d\alpha/dt$ were used in these calculations. $\tilde{\lambda}$ taken from tables in Cohen (1961); $\hat{h} = (N-n)/N$, $\hat{\gamma} = S^2/(\bar{X} - X_0)^2$, $\tilde{\mu} = \bar{X} + \hat{\gamma}(\bar{X} - X_0)$, and $\tilde{\sigma}^2 = S^2 + \hat{\gamma}(\bar{X} - X_0)^2$.

Length (cm)	Sample mean $\bar{X}$ (log rad/s)	Sample variance S^2	Sample range $(\bar{X} - X_0)$	$\hat{h}$	$\hat{\gamma}$	$\tilde{\lambda}$	$\tilde{\mu}$ (log rads/s)	$\tilde{\sigma}^2$	N
0.29	0.12	0.03	0.24	0.91	0.56	3.60	0.97	0.23	63
.32	.34	.19	.31	.96	2.00	4.31	1.65	.59	45
.39	−.64	.41	−.64	.93	.99	4.18	.86	.95	56
.40	.10	.08	.52	.87	.30	3.16	1.75	.93	79
.42	.17	.11	.36	.75	.87	2.23	.96	.39	32
.42	−.05	.07	.41	.91	.42	3.53	1.39	.65	45
.63	.33	.08	.44	.45	.47	.76	.65	.22	36
.83	−.08	.41	.63	.50	.40	.96	.58	.36	34
.95	−.12	.45	.30	.41	.47	.72	.33	.46	40
1.17	.14	.44	.42	.42	.46	.83	.39	.12	32

DISCUSSION

These experiments were performed to examine responses of northern anchovy larvae to attacks by biting (i.e., nonfilter-feeding) fish planktivores such as juvenile fish preying on zooplankters. The nature of the predator is relatively unimportant. Inexperienced larvae are likely to respond to an attack in the same way because in all cases failure to do so is terminal. The other alternative is that prey have specific predator images to which they respond, which seems improbable.

One objective was to evaluate an experimental technique that could be easily repeated and applied further (e.g., to problems of larval vulnerability and starvation interactions, effects of alternate prey species, prey density, and other questions affecting larval predation mortality). For this reason it was considered important initially to use a predator that was readily available at a uniform size. Natural fish predators could not be obtained in good condition and in a reasonable size range for the period of the experiment. Clown fish were found to be an excellent substitute.

However, experiments were performed at 20° C which is at the upper extreme of the temperature range of northern anchovy, but this probably had a small effect on the observations. The energy required for the short periods of high level activity in an escape swimming burst is undoubtedly derived mainly from anaerobic metabolism, which is known to be less dependent on temperature than aerobic metabolism (see, e.g., Bennett 1980). Experimental data on burst swimming performance are only available for rainbow trout and these data confirm the small effect of temperature in the range of 10° to 25° C (Webb 1978).

Two primary measures of response to attack were obtained, the proportion of larvae showing a startle response and the apparent looming threshold for that response. The proportion of larvae responding to attack increased linearly with length (Figure 1). This result is surprising. Kimmel (1972) has shown that several days are required for the Mauthner cell, which initiates the startle response, to extend caudally. The eyes are not functional before first feeding, so they could not initiate a startle response (O'Connell 1981). Neuromasts are present from hatching but if they were involved in stimulating a startle response, very high percentages of early larvae should show responses to attack. These developmental events suggest a rapid increase in percent response to attack would be expected in the yolk-sac stages, approaching maximum response levels at about first feeding, as found for responses to electric shock stimuli (Webb and Corolla 1981).

However, development rates are likely to vary widely in a population of larvae. It is for this reason that food is first added on the second day after hatching in spite of the fact that the mean time to first feeding is about 4 d (Hunter 1976). The percentage of yolk-sac larvae responding to attack was quite small and was probably due to early maturation (most likely of the visual system) of the most rapidly developing individuals.

The ALT changed with larval size, decreasing rapidly as larvae grew in length. This decline could have been due to improved acuity in the visual system and/or maturation of neural pathways processing visual information. This later could include shorter response latencies with age. The changes in ALT may be the basis for the increasing proportion of avoidance responses in larger larvae.

The only other measurement of looming thresholds for fish are those of Dill (1974a, b) for postlarval zebra danio, *Brachydanio rerio*, in re-

sponse to attacks by largemouth bass and to silhouettes. These data are not fully comparable with those obtained here for several reasons. First, the mean depth plus width was used to characterize the shape of the clown fish. Dill (1974a) used only width, citing reports that fish are more sensitive to horizontal movement than to vertical movement (Cronly-Dillon 1964; Jacobson and Gaze 1964). In contrast, operant conditioning experiments show that fish are particularly sensitive to apices (e.g., Hinde 1970; Baerends 1971) which occur at the dorsal and ventral margins of laterally compressed bodies. In the absence of definitive experiments relating shape to looming response thresholds, the mean value of depth plus width was considered most appropriate. Use of the mean value of depth and width would give larger values of $d\alpha/dt$ than use of depth alone (Equation (1)).

Second, the distance between the nose and the maximum depth and width of the predator was added to the reaction distance separating the predator and prey. This assumes that the prey either has depth vision or sees the equivalent of a silhouette of the predator. The inclusion of this term would reduce values of $d\alpha/dt$ compared with Dill's method.

The ALT values for postlarval zebra danios (2.0 cm long) was 0.43 rad/s. Northern anchovy larvae of the same size would be expected to have a mean value of about 0.6 rad/s from the relationship in Figure 6.

The overall function of the startle response is to avoid predators. How effective is it? The clown fish rarely pursued escaping larvae, although when they did so, the larvae were easily caught. In these experiments, chases may have been rare because larval densities were high. However, observations on adult piscivores attacking single prey show that chases are also rare with pike, *Esox* (Neill and Cullen 1974; Webb and Skadsen 1980), largemouth bass (Nyberg 1971; P. W. Webb unpubl. obs.), and rock bass, *Ambloplites rupestris* (P. W. Webb unpubl. obs.). Presumably the cost of pursuit is large relative to the benefits of capturing small prey particularly where there are alternative prey. In a normal planktonic assemblage, alternate prey could be important in reducing vulnerability of larval northern anchovy, especially in the presence of more opaque forms and those with more strongly pigmented eyes (Zaret and Kerfoot 1975).

Unfortunately, there are no field observations on larval responses to predation, and the likelihood of making the requisite field observations is remote. Nevertheless, the response of a prey to an attack is an obvious indicator of the prey's awareness and the possible difficulty of capture. The reluctance of many predators to attack responding prey, as noted above, together with the behavior of the clown fish observed in these experiments, imply that the startle response is an effective deterrent. Thus, it is most important that the larvae respond, but initially maximum swimming speeds are not required. Indeed the latter would be energetically more costly. Larvae clearly behave appropriately with a submaximal evasion (Figure 4), except when maximum performance becomes desirable in the rare event of a chase. Nevertheless, timing of the escape attempt must be accurate as 24 to 30% of the larvae attempted a response too late to escape capture.

Larval looming response thresholds will not only be important in escaping biting predators, but also other predation threats. Webb and Corolla (1981) discussed relationships between burst swimming performance of northern anchovy larvae and escape probabilities from plankton nets as a crude analogy with filter-feeding predators. While swimming performance could explain a large part of net avoidance, other factors were involved. Webb and Corolla suggested that declining response thresholds with experience would be important so that larger larvae responded earlier to an impending collision. The inverse relation between ALT with larval total length suggests that such changes occur. Presumably, similar thresholds or size relations would apply to larger predators. Then the reaction distance to a net moving, for example, at a given towing speed would be expected to be greater for larger northern anchovy larvae. This would contribute significantly to the size-dependent sampling bias of such nets.

This work has attempted to evaluate a method for quantifying responses of a fish larva to attacks by a predator as one step in studying the neglected aspect of predation on larval mortality. The advantages of the method are the visualization of both opaque and transparent individuals of small size and continuously recording their behavior. The disadvantages are that the space viewed must be small and hence only small predators can be used, and filtering predators are excluded. However, predation could be studied for particular feeders (e.g., biting fish and chaetognaths) arthropods (e.g., copepods and euphausids), and less discriminating feeders such as thaliaceans and

cnidarians. These are abundant in the plankton. In addition, effects of 1) larval density, 2) alternate prey in mixed planktonic assemblages, and 3) effects of starvation on larval vulnerability to predation could be studied.

ACKNOWLEDGMENTS

This work was completed while I was an NRC/NOAA Research Associate on leave from The University of Michigan. I wish to thank J. R. Hunter and R. Lasker for their hospitality and support. The Schlieren System was built by J. H. Taylor with partial support from a grant from the National Science Foundation (Grant No. DES75-04863) to R. Lasker and J. H. Taylor. Clown fish were provided by R. S. Keyes from Sea World, San Diego. I thank L. M. Dill, J. R. Hunter, R. Lasker, and P. Smith for their comments on the manuscript, and J. R. Zweifel for help in the statistical analysis.

LITERATURE CITED

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74:517-530.

BAERENDS, G. P.
1971. The ethological analysis of fish behavior. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. VI, p. 279-370. Acad. Press, N.Y.

BENNETT, A. F.
1980. The metabolic foundations of vertebrate behavior. Bioscience 30:452-456.

BLAXTER, J. H. S.
1969. Development: eggs and larvae. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. III, p. 177-252. Acad. Press, N.Y.

COHEN, A. C., JR.
1961. Tables for maximum likelihood estimates: singly truncated and singly censored samples. Technometrics 3:535-541.

CRONLY-DILLON, J. R.
1964. Units sensitive to direction of movement in goldfish optic tectum. Nature (Lond.) 203:214-215.

DILL, L. M.
1974a. The escape response of the zebra danio (*Brachydanio rerio*). I. The stimulus for escape. Anim. Behav. 22:711-722.
1974b. The escape response of the zebra danio (*Brachydanio rerio*). II. The effect of experience. Anim. Behav. 22.723-730.

EATON, R. C., R. D. FARLEY, C. B. KIMMEL, AND E. SCHABTACH.
1977. Functional development in the Mauthner cell system of embryos and larvae of the zebra fish. J. Neurobiol. 8:151-172.

GIBSON, J. J.
1980. The ecological approach to visual perception. Houghton Mifflin Co., Boston.

HINDE, R. A.
1970. Animal behavior. A synthesis of ethology and comparative psychology. 2d ed. McGraw-Hill, N.Y., 876 p.

HJORT, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 20, 228 p.

HOAR, W. S., AND D. J. RANDALL (editors).
1978. Fish physiology, Vol. VII. Acad. Press, N.Y., 576 p.

HOLDER, D. W., AND R. J. NORTH.
1963. Schlieren methods. HMO Stationary Office, Notes Appl. Sci. 48-120-31:1-106, Lond., Engl.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.
1977. Behavior and survival of northern anchovy *Engraulis mordax* larvae. Calif. Coop. Oceanic Fish. Invest. Rep. 19:138-146.
In press. The feeding behavior and ecology of marine fish larvae. *In* J. E. Bardach (editor), The physiological and behavioral manipulation of food fish as production and management tools. Int. Cent. Living Aquat. Res. Manage., Manila.

HUNTER, J. R., AND C. A. KIMBRELL.
1981. Egg cannibalism in the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 78:811-816.

JACOBSON, M., AND R. M. GAZE.
1964. Types of visual response from single units in the optic tectum and optic nerve of the goldfish. Q. J. Exp. Physiol. 49:199-209.

KIMMEL, C. B.
1972. Mauthner axons in living fish larvae. Dev. Biol. 27:272-275.

LASKER, R.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:212-230.

LEONG, R. J., AND C. P. O'CONNELL.
1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Board Can. 26:557-582.

LILLELUND, K., AND R. LASKER.
1971. Laboratory studies of predation by marine copepods on fish larvae. Fish. Bull., U.S. 69:655-667.

NEILL, S. R. ST. J., AND J. M. CULLEN.
1974. Experiments on whether schooling by their prey affects the hunting behavior of cephalopods and fish predators. J. Zool. (Lond.) 172:549-569.

NYBERG, D. W.
1971. Prey capture in the largemouth bass. Am. Midl. Nat. 86:128-144.

O'CONNELL, C. P.
1981. Development of organ systems in the northern anchovy, *Engraulis mordax*, and other teleosts. Am. Zool. 21:429-446.

RAND, D. M., AND G. V. LAUDER.
In press. Prey capture in the chain pickerel *Esox niger*:

correlations between feeding and locomotor behavior. Can. J. Zool.

RICKER, W. E.
1979. Growth rates and models. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. VIII, p. 677-743. Acad. Press, N.Y.

SPRAGUE, J. B.
1969. Review paper: Measurement of pollutant toxicity to fish. I. Bioassay methods for acute toxicity. Water Res. 3:793-821.

THEILACKER, G. H., AND R. LASKER.
1974. Laboratory studies of predation by euphausiid shrimps on fish larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 287-299. Springer-Verlag, Berl.

TREISMAN, M.
1975. Predation and the evolution of gregariousness. II. An economic model for predator-prey interaction. Anim. Behav. 23:801-825.

VON WESTERNHAGEN, H., AND H. ROSENTHAL.
1976. Predator-prey relationship between Pacific herring, *Clupea harengus pallasi*, larvae and a predatory hyperiid amphipod, *Hyperoche medusarum*. Fish. Bull., U.S. 74:669-674.

WEBB, P. W.
1978. Temperature effects on acceleration of rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 35:1417-1422.

WEBB, P. W., AND R. T. COROLLA.
1981. Burst swimming performance of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 79:143-150.

WEBB, P. W., AND J. M. SKADSEN.
1980. Strike tactics of *Esox*. Can. J. Zool. 58:1462-1469.

ZARET, T. M., AND W. C. KERFOOT.
1975. Fish predation on *Bosmina longirostris*: body-size selection *versus* visibility selection. Ecology 56:232-237.

GULF OF MEXICO SHRIMP PRODUCTION: A FOOD WEB HYPOTHESIS[1]

R. WARREN FLINT AND NANCY N. RABALAIS[2]

ABSTRACT

The desire to better understand the dynamics of commercial shrimp populations which support an important regional fishery on the south Texas outer continental shelf stimulated us to investigate an extensive data base for links in the various ecosystem components that related to these dynamics. A correlational model was developed that suggested relationships between pelagic and benthic components of the south Texas marine ecosystem. Utilizing tracers, such as nickel concentrations in biota, sediment, and water, we identified pathways of natural transfer between zooplankton, the benthos, and coastal shrimp populations. These results stimulated us to develop a theoretical food web for the shrimp populations, focusing on transfer of carbon. The results of this exercise indicated that the majority of primary production (approximately 80%) is diverted to the benthos. Furthermore, it appeared that the secondary production of benthic infauna was not sufficient to alone support the coastal shrimp populations. We concluded that at least part of their nutrition was derived from the detritus pool which was maintained by the excessive amount of primary production diverted to the benthos. The evidence presented here suggests that the marine ecosystem in the coastal waters of south Texas functions differently than other ecosystems studied in recent years and pinpoints the need for a better understanding of the basis upon which our marine living resources are supported, in order to predict not only fishery yields but also effects of environmental disturbance.

The commercial shrimp fishery in the U.S. waters of the Gulf of Mexico is one of the most productive fisheries the United States pursues. This fishery provides better than 20% of the gross dollar value for the total U.S. harvest (U.S. National Marine Fisheries Service 1976) and represents the largest fishery in terms of weight harvested and effort expended along the gulf coast. For example, from a coastal area of Texas covering 10,000 km^2, an average of 5.7×10^6 kg/yr of brown shrimp, *Penaeus aztecus*, was landed in 1975-76, which represented an annual value of $18 million. A decline in this fishery could cause economic loss, at least on a regional scale.

Research emphasis on the populations of penaeid shrimp that support the commercial fishery in the northwestern Gulf of Mexico has been directed towards laboratory behavioral studies, migratory habits, and the development of models relating harvest to environmental factors and management strategies. Although the data derived from these studies contribute to our understanding of the natural fluctuations that occur in the fishery, they do not provide adequate information about where the penaeid populations fit into the trophic structure of the marine ecosystem and how these populations function. Due to this lack of knowledge, environmental managers would not be able to predict with confidence how a major perturbation in the Gulf of Mexico would affect the shrimp populations.

For years information has been accumulating on primary production, zooplankton biomass, and the distribution of benthic fauna in important marine fishery areas. Attempts to quantify links between these components have been provided by Steele (1974) for the North Sea ecosystem and by Mills and Fournier (1979) for the Scotian shelf. Arntz (1980) more recently attempted to relate benthic production with that of commercially important demersal fishes in the Baltic Sea. With the completion of a 3-yr multidisciplinary environmental study of the south Texas continental shelf (Flint and Rabalais 1981), one more fishing area has been characterized.

The Texas shelf ecosystem is a dynamic system driven by a complex aggregation of meteorologic and oceanographic events. Superimposed upon these phenomena are influences from local rivers and estuaries as well as from distant points such as the Mississippi River and the deep oceanic waters of the gulf basin (Flint and Rabalais 1981). The shallower waters of the Texas shelf are biologically a critical part of this ecosystem because of

[1]The University of Texas Marine Science Institute Contribution No. 503.

[2]University of Texas Marine Science Institute, Port Aransas Marine Laboratory, Port Aransas, TX 78373.

Manuscript accepted May 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

their larger standing crops of phytoplankton, zooplankton, and benthos (Flint and Rabalais 1981) which are capable of supporting the large shrimp fishery yield in these waters.

Based upon a desire to better understand the characteristics of an important resource of the Texas continental shelf, we used the south Texas environmental study data as well as information from the published literature to develop a model of the trophic relationships supporting the brown shrimp fishery. This analysis provided insight into the general structure of marine ecosystems which support fisheries. It also provided the necessary data to judge whether the generalization of Dickie (1972) and Mills (1975)—that despite geographic differences most coastal ecosystems with productive fisheries have similarly constructed food webs—is well founded or not.

METHODS

A multidisciplinary research program (1975-77) was conducted on the south Texas outer continental shelf (STOCS) at 25 stations (Figure 1). The study included water mass characterization, pelagic primary and secondary production as described by floral and faunal biomass, and benthic productivity as described by macroinvertebrate infaunal and epifaunal densities as well as demersal fish densities and biomass. The study, summarized by Flint and Rabalais (1981), provided a data base depicting the general characteristics of a marine subtidal area with important natural resources.

The focus of the results presented in this paper is on data collected from a "Reference Station" (Figure 1) which we consider representative of Statis-

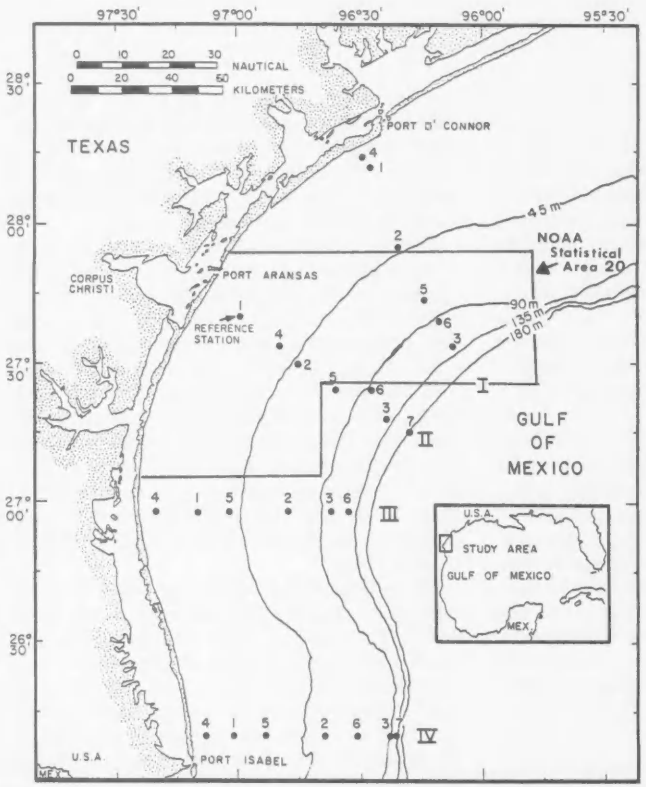

FIGURE 1.—Map of the south Texas continental shelf with location of sampling sites for 1975-77 environmental study. NOAA shrimp catch Statistical Area 20 is superimposed along with the Reference Station representing the source of data used in the text.

tical Area 20, the shrimp landing reporting region (U.S. National Marine Fisheries Service 1978) most closely associated with the STOCS study area. As mentioned previously, the shallower waters of the south Texas shelf are more productive, and the maximum yield of the brown shrimp fishery is within the depth range of this station (Grant and Griffin 1979). This site was characterized by one of the largest data bases of all 25 stations. Water column variables were sampled monthly during 9 mo in 1976 and 1977, and benthic variables were sampled monthly during 9 mo in 1976 and seasonally (winter, spring, and fall) in 1977. Details of sampling procedures are available in Flint and Rabalais.[3]

The STOCS data base contained adequate data on various biotic and abiotic components to allow for an integrated investigation of ecosystem relationships, with the shrimp populations as the ultimate focus of this exercise. Our approach was twofold. In the first step, we evaluated all variables in relation to one another using a correlation matrix. These comparisons included components within the pelagic environment, within the benthic environment, and between the two environments. Variables considered were similar to those listed in table 3 of Flint and Rabalais (1981). We looked for relative changes in population densities and biomass of biota that might be expected to be associated, such as phytoplankton and zooplankton or brown shrimp and benthic macroinfauna. Also, tracers, such as hydrocarbons and trace metals, identified relationships between components of the ecosystem based on organism body burdens and concentrations of the tracers in water samples and sediments.

Bivariate Pearson correlation coefficients were used (Sokal and Rohlf 1969). All correlation coefficients, either positive or negative, were evaluated for their biological meaning. Those suspected of ecosystem relationships were put in a two-by-two correlation matrix, within which the number of significant correlations ($P<0.01$) had to be more than 5% of the total for us to conclude that they were not chance produced (Bernstein et al. 1978).

The goal of this first step was to develop a correlational model of relationships in the data that suggested patterns in trophic coupling between shrimp populations and other biotic components. The patterns derived in step one prompted us to develop biomass estimates for the related components. The goal of the second step was to develop a theoretical model of energy flow in a trophic web which included penaeid shrimp as our central focus. Data from the STOCS Reference Station were used to estimate floral and faunal biomass as follows.

Chlorophyll *a* was measured according to standard techniques (Strickland and Parsons 1968). Biomass of zooplankton was determined from oblique (surface to near bottom to surface) tow samples taken with a 1 m net of 223 μm mesh. Neuston biomass was determined from samples collected in a 505 μm mesh neuston net towed in surface waters for 15 min. Zooplankton and neuston data were originally reported as ash-free dry weights but were converted to wet weights using a conversion factor of 0.15 for crustaceans (Lie 1968). Microplankton samples were collected in a 50 l Niskin bottle at the surface and at one-half the depth of the photic zone. Wet weight biomass was estimated by measuring volume displacement and assuming that a cell density of 1 μ^3 equalled 10^{-6} μg wet weight.

Benthic macroinfauna (>0.5 mm) samples were taken with a 0.1 m Smith-McIntyre grab. Estimates of benthic infaunal biomass (Table 1) in the south Texas shelf area ranged between 0.5 g/m^2

[3]Flint, R. W., and N. N. Rabalais (editors). 1980. Environmental studies, south Texas outer continental shelf, 1975-1977. Vol. III. Final report to the Bureau of Land Management, Department of the Interior, Wash., D.C. Contract AA551-CT8-51, 648 p.

TABLE 1.—Comparison of abundance and biomass of macrobenthos from the northwestern Atlantic Ocean and northwestern Gulf of Mexico.

Atlantic Ocean[1]			Gulf of Mexico				
Depth	Density (no./m^2)	Wet weight (g/m^2)	Depth	Density[1] (no./m^2)	Wet weight[1] (g/m^2)	Density[2] (no./m^2)	Wet weight[3] (g/m^2)
30	26,060	7.69	12			1,536	0.63
40	7,390	2.44	16	1,373	0.74		
			30	14,623	4.09	675	0.28
Average	16,725	5.07		7,998	2.42	1,106	0.46

[1]Measures from Rowe et al. (1974).
[2]Measures from the South Texas Outer Continental Shelf Study, 1975-77.
[3]Wet weight calculated from densities of organisms using the density to wet weight ratio of the respective values from Rowe et al. (1974).

(STOCS study) and 2.4 g/m^2 (Rowe et al. 1974). Since the data from Rowe et al. (1974) were based on a single sampling effort and the measures from the south Texas study were based on 12 separate sampling periods, we biased our infaunal biomass estimates towards the STOCS data and derived a biomass figure from a regression between total density and total biomass of infaunal samples (Table 1). Epifaunal invertebrates and demersal fish were sampled in 15-min bottom tows with a 10.7 m Texas box otter trawl with a 25 mm stretched mesh cod end. Wet weights were determined directly from the trawl samples.

Because biomass measurements were made on the penaeid shrimp during only one season in the whole STOCS study, we felt the data were not sufficient to completely characterize the biomass levels for the shrimp. Thus, shrimp biomass data were taken from Gulf Coast Annual Shrimp Landing Reports (U.S. National Marine Fisheries Service 1976, 1978). The shrimp fishery yields, however, did not represent the total production of shrimp in the coastal gulf waters. Therefore, for our model we estimated the biomass of shrimp populations that was not reflected by the catch statistics. A survival curve for the shrimp population was calculated (Figure 2), based upon a total population egg production rate of 10^{11} [based on a mean of 800,000 eggs/adult female >140 mm total length and a 1:1 sex ratio (Pérez Farfante 1969)] with a survival rate for the hatch of 1%. This resulted in a recruitment rate of 10^5 juveniles to the population (Figure 2). The three additional data points on the curve were determined by splitting the shrimp biomass from the catch statistics (shaded area) into three size classes and calculating the number of shrimp of mean size within each of these classes. The curve was then extrapolated from recruitment through each of these data points with the mean size at emigration from the bays indicated (Figure 2).

The results of this two-step exercise provided information to estimate production and develop an energy flow model for the components of the south Texas shelf food web according to the ideas of Steele (1974) and Mills and Fournier (1979). Primary production estimates on an annual basis were calculated from chlorophyll *a* measurements according to the methods of Ryther and Yentsch (1957). A turnover ratio of 7 was used to convert macrozooplankton standing stocks to annual production (Steele 1974). Certain factors, such as tows failing to reach the bottom and net clogging causing <100% efficiency, contribute known biases to zooplankton sampling methods (Hopkins 1963; Wiebe and Holland 1968; Fasham 1978). Because of this and the fact that the water column was usually homogeneous in the shallow waters at the Reference Station (Flint and Rabalais 1981), we doubled the zooplankton production estimates. A turnover ratio of 10 was used for the microzooplankton standing stocks because we assumed a

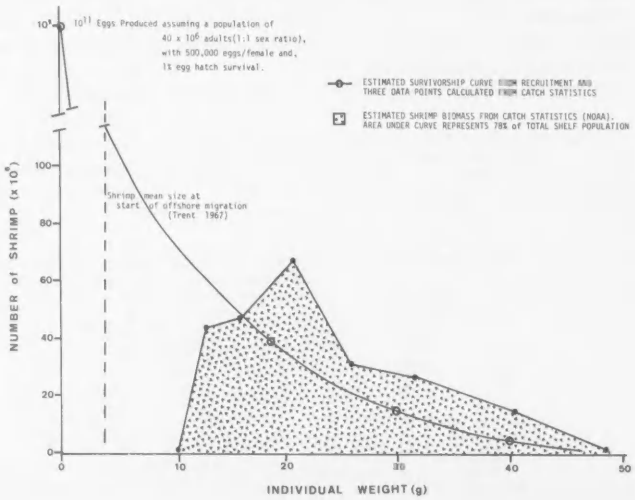
10^{11} Eggs Produced assuming a population of 40 x 10^6 adults(1:1 sex ratio), with 500,000 eggs/female and, 1% egg hatch survival.
ESTIMATED SURVIVORSHIP CURVE FROM RECRUITMENT AND THREE DATA POINTS CALCULATED FROM CATCH STATISTICS
ESTIMATED SHRIMP BIOMASS FROM CATCH STATISTICS (NOAA). AREA UNDER CURVE REPRESENTS 78% of TOTAL SHELF POPULATION
Shrimp mean size at start of offshore migration (Trent 1967)
NUMBER of SHRIMP (x 10^6)
INDIVIDUAL WEIGHT (g)
0
20
40
60
80
100
10
30
50

FIGURE 2.—Plot of the reported shrimp (*Penaeus aztecus*) fishery yield according to size class (shaded area) along with an estimated survivorship curve (solid line) for the south Texas continental shelf from NOAA Statistical Area 20 (see Figure 1).

larger ratio for the smaller sized microplankton as found by Droop and Scott (1978) and Mills and Fournier (1979). Benthos standing stocks were converted to annual production using a turnover ratio of 4.5 (Nichols 1977; Arntz 1980). A conversion for heads-on weight (1.61) and a turnover ratio of 0.8 (E. Klima[4]) were used to determine annual production from estimated shrimp standing stocks. A 6% conversion between wet weight and carbon content of metazoans (G. T. Rowe[5]) was used to determine carbon equivalents of annual production estimates.

RESULTS

Correlational Model

Significant correlation coefficients identified in the bivariate correlation analysis along with relationships in the data that suggested patterns in trophic coupling were used to develop the model illustrated in Figure 3. There was a relationship between the water column fauna, in this case zooplankton, and the sediment detritus pool as evidenced by the correlations between zooplankton nickel body burdens and sediment nickel concentrations as well as several zooplankton hydrocarbon body burden variables and hydrocarbons observed in the sediment (Figure 3). The analysis further indicated that primary producer biomass, represented by bottom water chlorophyll *a* concentrations, was related to density changes in benthic macroinfauna, potentially through the detritus pool (Figure 3). Relationships also existed between sediment hydrocarbon concentrations and bacterial density, indicating another potential link through the detritus pool.

Within the benthos, meiofaunal and macroinfaunal densities were correlated to bacterial densities, and macroinfaunal densities were correlated with meiofaunal densities (Figure 3). The constant ratio of benthic faunal densities to bacteria and not organic carbon (Figure 3) suggested

[4]E. Klima, Director, Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA, 4700 U Street, Galveston, TX 77550, pers. commun. August 1980.

[5]G. T. Rowe, Research Scientist, Brookhaven National Laboratory, Upton, Long Island, NY 11973, pers. commun. June 1980.

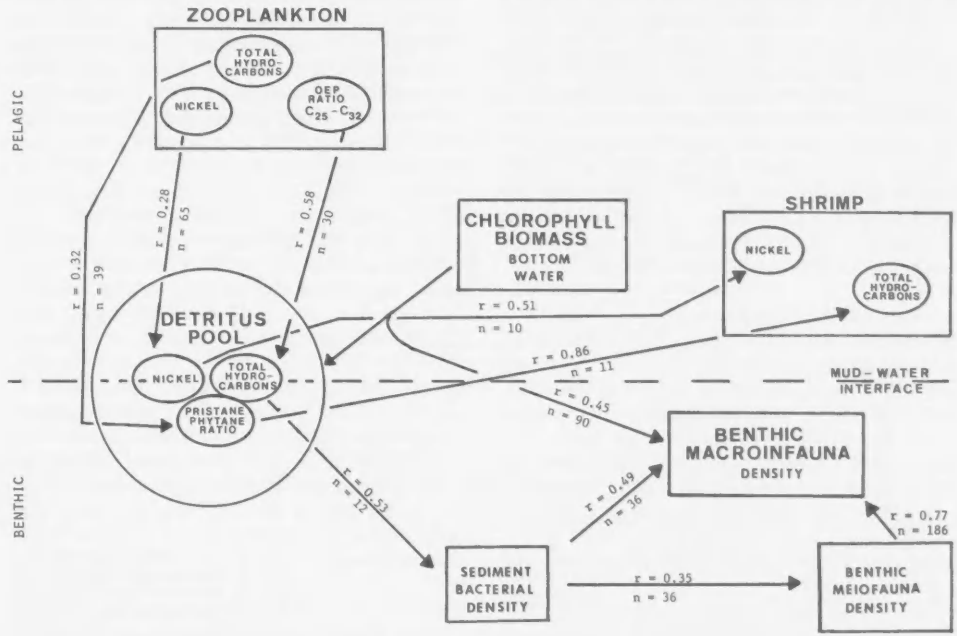

FIGURE 3.—Schematic representation of significant ($P<0.01$) correlation coefficients (r) found between south Texas continental shelf environmental variables measured for 1976-77. Sample size (n) is also shown for each correlation.

bacteria as a food source. The meiofauna-macrofauna correlation completed the trophic web between the sediment inhabitants.

Finally, densities of shrimp on the Texas shelf were tied to the sediment detritus pool by correlations between shrimp body burdens of nickel and total hydrocarbons and sediment nickel concentrations and a sediment hydrocarbon variable (Figure 3). The correlations between zooplankton nickel body burdens, nickel concentrations in the sediment, and shrimp nickel body burdens (Figure 3) allowed us to propose a trophic coupling hypothesis for the shelf shrimp populations that included both pelagic and benthic components.

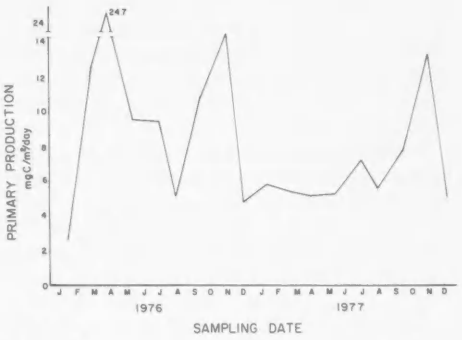

FIGURE 4.—The 2-yr cycle of primary production (carbon fixation) for Texas coastal waters between 1976 and 1977. Primary production calculated according to methods of Ryther and Yentsch (1957) using chlorophyll *a* measurements.

Trophic Web

Primary production for Texas inner shelf waters, determined from the Reference Station chlorophyll *a* measurements, was bimodal annually with peaks usually occurring in spring and fall (Figure 4). Since the spring peak in biomass for 1977 was not measured and presumably missed by the timing of our sampling, the estimate of 103 g C/m^2 per yr representing the amount of carbon fixed in the primary level of the trophic web (Figure 5) was probably low.

Macrozooplankton biomass on the Texas shelf averaged 3.57 g/m^2 wet weight (Table 2). From this amount, annual production of macrozooplankton was estimated to be 24.98 g/m^2 per yr. In conversion for sampling bias, the production estimate was doubled to 49.96 g/m^2 per yr. The carbon equivalent of zooplankton production was estimated to be 3 g C/m^2 per yr. Similarly converted biomass data from the neuston component of the planktonic community added 0.2 g C/m^2 per yr (Table 2) to the macrozooplankton portion of the trophic web (Figure 5). Standing stock of microzooplankton was 0.47 g/m^2 wet weight which converted to an annual production of 0.9 g C/m^2

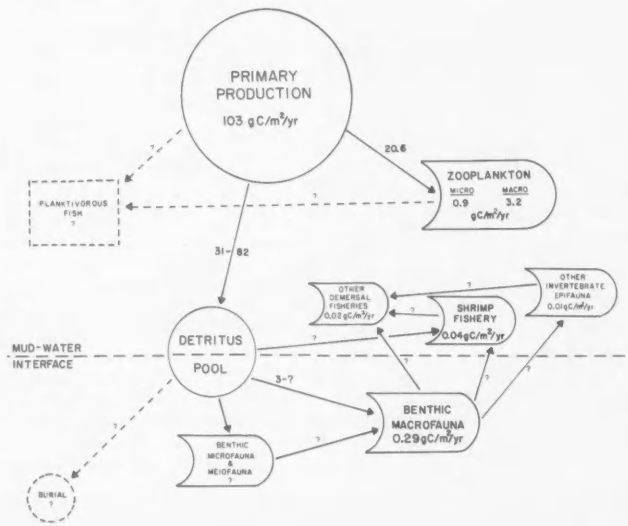

FIGURE 5.—Theoretical model of an annual production and energy flow food web for the south Texas continental shelf. All material flows represent gram C/square meter per year.

TABLE 2.—Procedures for calculating the amount of annual production for zooplankton components.

Macroplankton: Zooplankton biomass (wet weight)	3.57 g/m²	assume → TR = 7[1]	24.98 g/m² per yr	sampling → bias conversion	49.96 g/m² per yr	assume carbon → equivalent = 6% wet weight[2]	3.0 g C/m² per yr
Neuston biomass (wet weight)	0.16 g/m²	assume → TR = 7[1]	1.13 g/m² per yr	sampling → bias conversion	3.40 g/m² per yr	assume carbon → equivalent = 6% wet weight[2]	0.2 g C/m² per yr
Microplankton: biomass (wet weight)	0.47 g/m²	assume → TR = 3[3]10	4.65 g/m² per yr	sampling → bias conversion	13.96 g/m² per yr	assume carbon → equivalent = 6% wet weight[2]	0.9 g C/m² per yr
						Total	4.1 g C/m² per yr

[1]Turnover ratio (TR) for zooplankton from Steele (1974).
[2]Assume carbon equivalent equal to 6% wet weight for metazoans (G. T. Rowe pers. commun).
[3]Assume higher turnover ratio for microplankton than TR = 7 from Steele (1974).

per yr (Table 2). The estimated total production for the zooplankton components of the food web on the inner Texas shelf was 4.1 g C/m² per yr (Table 2, Figure 5).

If we assume a minimum transfer efficiency of 20% between primary producers and zooplankton as suggested by Steele (1974), which is more conservative than the 27-32% suggested by Mills and Fournier (1979), then 20.6 g C/m² per yr (Figure 5) would be required to support these fauna and 82 g C/m² per yr of primary production would remain. With the exception of a small proportion of this 82 g C/m² per yr, which may support pelagic planktivorous fish, we believe that the majority of the primary production is directed elsewhere.

We derived a biomass figure for the benthic macroinfauna of 1.1 g/m² which we then converted to an annual production of 0.29 g C/m² per yr (Figure 5). From shrimp catch statistics, we estimated shrimp production at 0.03 g C/m² per yr. Based on the hypothesized survival curve (Figure 2), the estimate of shrimp production from catch statistics was found to represent 78% of the actual shelf population production as indicated by the shaded area under the curve. Therefore, with the additional 22% of unharvested shrimp biomass, the annual shrimp production was 0.04 g C/m² per yr (Figure 5). Additional data from the STOCS study indicated that demersal fish and invertebrate epifauna composed 0.02 and 0.01 g C/m² per yr production, respectively (Figure 5). The combination of these amounts with the shrimp production estimates accounted for 0.07 g C/m² per yr produced by fauna living in the bottom waters. Comparing this trophic level with the infaunal production (0.29 g C/m² per yr) and assuming a 10% transfer efficiency, benthic infaunal production appears to be an insufficient food source to solely support the demersal component of the inner shelf food web.

DISCUSSION

Research emphasis on the populations of shrimp that are fished in the gulf has been directed towards migratory habits (e.g., Inglis 1960; Klima 1964; Kutkuhn 1966; Trent 1967), dockside catch statistics (e.g., Gunter 1962; Caillouet and Patella 1978; U.S. National Marine Fisheries Service 1978), the development of models relating fishery harvest to environmental factors such as freshwater inflow (e.g., Hildebrand and Gunter 1952; Martin et al. 1980), and natural history (e.g., Heegard 1953; Iversen and Idyll 1960; St. Amant et al. 1966). Other studies have focused on behavior under laboratory conditions (e.g., Aldrich et al. 1968; Lakshmi et al. 1976). More recently, simulation of the shrimp fishery emphasizing different management strategies has been attempted by Grant and Griffin (1979). These studies, however, fail to pinpoint which factors maintain the shrimp production which supports a thriving fishery. Sources and pathways of nutrition and ramifications of interruption of this flow still remain to be determined.

Other recent studies on important fishery areas (Steele 1974; Mills and Fournier 1979; Arntz 1980) point out the need to understand the general structure of marine ecosystems and the trophic webs which support species important to fisheries. Our study consolidates information on primary production, secondary production, and abundance of benthic animals into a theoretical model of the northwestern gulf shrimp fishery food web.

The Texas shelf supports large phytoplankton biomasses with high annual production, especially in inner shelf waters where plankton are most abundant (Figure 6). Spring blooms in phytoplankton biomass are correlated with riverine inputs and nutrient maxima (Flint and Rabalais 1981). The patterns of inner shelf phyto-

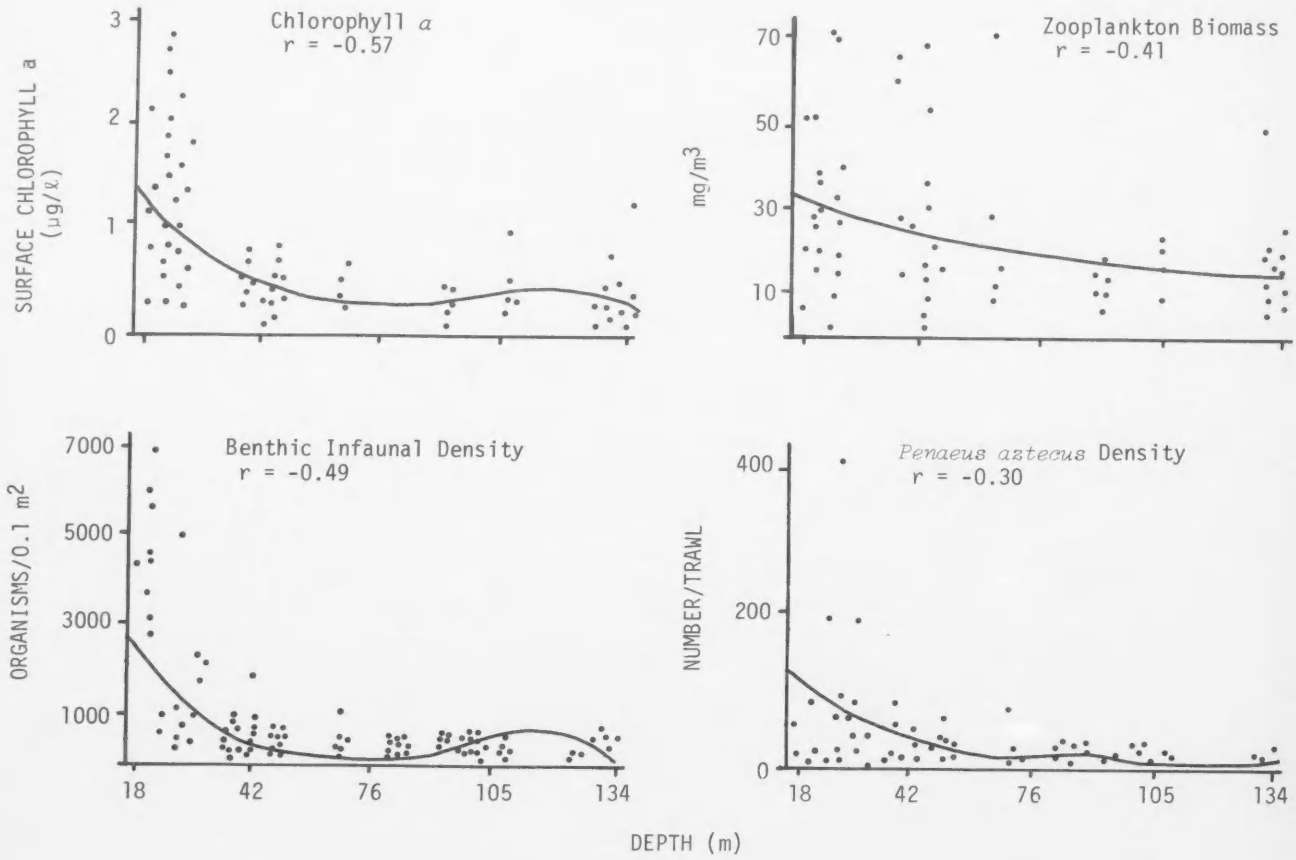

FIGURE 6.—Chlorophyll *a*, zooplankton biomass, benthic infaunal density, and shrimp (*Penaeus aztecus*) density for the south Texas continental shelf study 1976-77. Best fit fourth order polynomial regression lines are presented along with the significant ($P<0.05$) correlation coefficients (r) (from Flint and Rabalais 1981).

plankton productivity are paralleled by zooplankton biomass (Figure 6) with peaks in shallow waters and decreases in an offshore direction. Likewise, both infaunal and epifaunal (represented by *P. aztecus*) benthic organisms are more numerous along the inner shelf (Figure 6) where general productivity is greatest in response to larger food supplies, greater habitat heterogeneity, and nutrients. These productive shallow waters are critical to the shrimp fishery populations. Greatest shrimp harvests for this part of the Gulf of Mexico are recorded for these shallow waters (Grant and Griffin 1979).

Although our estimate of primary production (103 g C/m^2 per yr) may be low because one spring bloom (1977) was missed by sampling frequency, this value is similar to values reported for other fish-producing areas. Mills and Fournier (1979) reported 102 and 128 g C/m^2 per yr for the Scotian shelf and slope, respectively, and Steele (1974) reported 90 g C/m^2 per yr for the North Sea ecosystem. With the exception of a small portion which may support pelagic planktivorous fish, we believe that the majority of the northwestern gulf primary production is directed to the bottom. The amount of pelagic fish production supported by primary production on the Texas inner shelf is unknown; however, the amount of zooplankton biomass measured is not sufficient to support large populations of pelagic planktivorous fish. As indicated by the lack of a commercial fishery, the planktivorous fish that primary production could support represent small standing stocks in this area of the Gulf of Mexico. Thus, almost 80% of the total primary production biomass remains and presumably much of this reaches the bottom in coastal waters.

Further evidence for this conclusion is shown by the phytoplankton biomass distributions in the water column (Figure 7). The bottom waters support equal or greater biomass of primary producers than the surface or middepth waters as

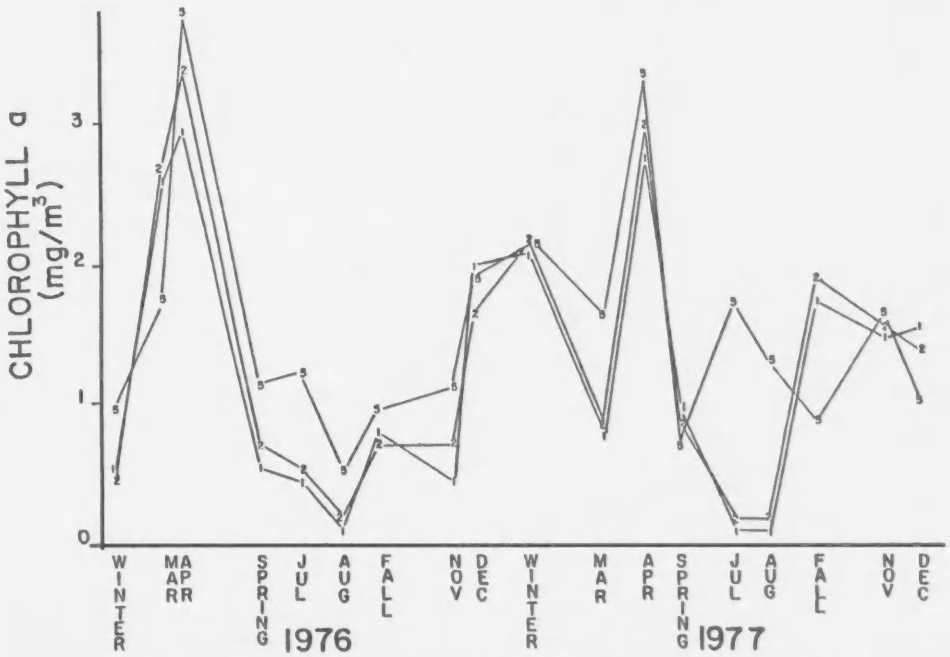

FIGURE 7.—Plot of surface (1), one-half the depth of the photic zone (2), and bottom (5) water chlorophyll *a* concentrations for the south Texas continental shelf environmental study between 1976 and 1977 at the Reference Station in Figure 1 (from Kamykowski, D.L., and S. Milton. 1980. Phytoplankton and productivity. *In* R. W. Flint and N. N. Rabalais (editors), Environmental studies, south Texas outer continental shelf, 1975-1977, Vol. III, p. 231-284. Final report to the Bureau of Land Management, Wash., D.C. Contract AA551-CT8-51).

shown by the chlorophyll *a* concentrations in the water column (Figure 7). These increases with depth indicate that much of what is produced in the pelagic zone reaches the bottom and accumulates.

The lack of stratification of the water column on the inner shelf during most of the year makes this conclusion reasonable. The water column is almost always well mixed in shallower waters <30 m depth (Flint and Rabalais 1981, figure 4), allowing for a direct transport of photic zone primary production to the bottom. This characteristic is also ideal for processes related to benthic-pelagic coupling, which we suspect are important in this coastal ecosystem.

Because mixing in the shallow shelf waters results in a relatively homogeneous water column, it is reasonable to propose a trophic coupling hypothesis for shrimp which includes both pelagic and benthic components. The relationships based on nickel tracers (zooplankton→sediment→shrimp) support this scheme. Also, zooplankton fecal pellets are a major input to the marine detritus pool (Cushing 1966; Steele 1974). Under the hydrographic conditions present, the discrimination between pelagic and benthic parts of the ecosystem is decreased and the potential for trophic coupling between the sea floor and overlying waters becomes more meaningful.

A key question about shrimp production concerns the component(s) of the benthic community from which shrimp derive their nutrition. Several studies have attempted to determine the role of benthic infauna as a food source for commercially important demersal species. Boesch (in press) found alterations in macrobenthic communities that resulted in reductions in populations which were dominant food items for demersal fishes and invertebrates. However, the contribution of energy flow to higher trophic levels from these populations and whether the larger fish and invertebrates were severely affected were unknown. Additional observations such as those of McIntyre et al. (1970) on molluscan siphon cropping by a commercially important fish species, and Arntz (1980) on changes in benthic infaunal biomass directly associated with demersal fish predation, implicate the benthos as important food items for species of commercial value.

Based upon our theoretical model of production estimates and energy flow for the south Texas coastal environment, benthic infaunal production appears to be an insufficient food source to solely support the demersal component of the inner shelf food web. If we assume a minimum 10% transfer efficiency for the infaunal biomass produced, which is 0.29 g C/m^2 per yr, this trophic level could not support the 0.07 g C/m^2 per yr of total production by fish, shrimp, and other invertebrates, nor the 0.04 g C/m^2 per yr annual production of *P. aztecus*. Our calculations do not include meiofauna production. Even if this component were known, there probably would still not be enough carbon production by fauna in the benthos to directly support all higher trophic levels in the bottom waters. In addition, the correlation analysis did not identify any significant correlations between shrimp densities and densities of fauna inhabiting the sediment.

The correlations between shrimp body burdens and tracers in the sediment, however, provide evidence for another means of shrimp gaining nutrition, the detritus pool. These correlations support conclusions from other studies (Cook and Lindner 1970; Caillouet et al. 1976) that shrimp rely upon food provided by the marine detritus pool for at least some of their nutrition. Condry et al. (1972) observed that brown shrimp ate dead diatoms and algal mat material in an estuarine habitat. Moriarty (1977) recorded microbial feeding by shrimp from detritus substrates, and Foulds and Mann (1978) found evidence that crustaceans are able to digest cellulose. The dependence of these populations on the detritus pool is a reasonable conclusion.

Another potential contribution to the detritus pool comes from the discards—small shrimp, fish, and other invertebrates—from the methods of harvest employed by the shrimp fishery. According to Bryan and Cody,[6] approximately 116 million kg of catch-associated organisms are discarded annually on the shelf off south Texas. Most of this material eventually reaches the bottom and becomes an additional source of food for scavengers, such as shrimp, to supplement the food sources from the benthic habitat.

The theoretical food web we propose for the penaeid shrimp fishery of the shallow nearshore waters of the south Texas continental shelf is in contrast to the food web described by Steele (1974) for the North Sea ecosystem and its related

[6]Bryan, C. E., and T. J. Cody. 1975. Discarding of shrimp and associated organisms on the Texas brown shrimp (*Penaeus aztecus*) grounds. Final Rep. to Texas Parks and Wildlife Department PL88-309, Project 2-276R, 38 p.

fisheries. Whereas we propose a detrital-based food web dependent on about 80% of the primary producer biomass being directed to the bottom, Steele (1974) indicated that only 30% of the primary production reached the benthos in the North Sea. On the other hand, Mills and Fournier (1979) observed that the majority of primary production was diverted to the bottom on the Scotian shelf. This primary production, however, was not adequate to satisfy the requirements of the benthic or pelagic food chains. The importance of herbivorous zooplankton and secondary consumers, such as ctenophores and chaetognaths, was emphasized by Mills and Fournier as elements potentially characterizing the structure of energy transfer in the Scotian shelf ecosystem. From the evidence available, the inner shelf ecosystem of the northwestern Gulf of Mexico, with its food webs leading to commercially important penaeid shrimp, appears different in structure from other areas with major commercial fisheries. The concept that food webs leading to these fishery populations are similarly constructed is not supported by our study, which only further points out what Mills and Fournier (1979) emphasized—detailed regional studies are needed before predictive models can be developed for these fisheries.

Our theoretical model of the trophic structure supporting the penaeid populations in the northwestern Gulf of Mexico is an approach to the detailed regional studies that are necessary. Much still needs to be done to define the pathways of nutrition and the implications of these pathways being interrupted by major environmental disturbances. Research on shrimp migratory patterns, behavior, response to environmental factors, and fishery statistics alone will not provide adequate information about the functioning of an ecosystem with respect to the trophic structure supporting a commercial fishery. Our study pinpoints some of the potential pathways of energy flow. The need for research to define the functioning of the ecosystem of which penaeid shrimps are a part cannot be overemphasized.

LITERATURE CITED

ALDRICH, D. V., C. E. WOOD, AND K. N. BAXTER.
1968. An ecological interpretation of low temperature responses in *Penaeus aztecus* and *P. setiferus* postlarvae. Bull. Mar. Sci. 18:61-71.

ARNTZ, W. E.
1980. Predation by demersal fish and its impact on the dynamics of macrobenthos. *In* K. R. Tenore and B. C. Coull (editors), Marine benthic dynamics, p. 121-150. Univ. S.C. Press, Columbia.

BERNSTEIN, B. B., R. R. HESSLER, R. SMITH, AND P. A. JUMARS.
1978. Spatial dispersion of benthic Foraminifera in the abyssal central North Pacific. Limnol. Oceanogr. 23:401-416.

BOESCH, D. F.
In press. Ecosystem consequences of alterations of benthic community structure and function in the New York Bight region. *In* G. Mayer (editor), Ecological effects of environmental stress, New York Bight. Univ. South Carolina Press, Columbia.

CAILLOUET, C. W., AND F. J. PATELLA.
1978. Relationship between size composition and ex-vessel value of reported shrimp catches from two Gulf Coast States with different harvesting strategies. Mar. Fish. Rev. 40(2):14-18.

CAILLOUET, C. W., J. P. NORRIS, E. J. HEALD, AND D. C. TABB.
1976. Growth and yield of pink shrimp (*Penaeus duorarum duorarum*) in feeding experiments in concrete tanks. Trans. Am. Fish. Soc. 105:259-266.

CONDREY, R. E., J. G. GOSSELINK, AND H. J. BENNETT.
1972. Comparison of the assimilation of different diets by *P. setiferus* and *P. aztecus*. Fish. Bull., U.S. 70:1281-1292.

COOK, H. L., AND M. J. LINDNER.
1970. Synopsis of biological data on the brown shrimp *Penaeus aztecus aztecus* Ives, 1891. FAO Fish. Rep. 57:1471-1497.

CUSHING, D. H.
1966. Models of the productive cycle in the sea. *In* Morning review lectures, p. 103-115. Sec. Int. Oceanogr. Conf., UNESCO, Moscow.

DICKIE, L. M.
1972. Food chains and fish production. Int. Comm. N. Atl. Fish. Spec. Publ. 8:201-221.

DROOP, M. R., AND J. M. SCOTT.
1978. Steady-state energetics of a planktonic herbivore. J. Mar. Biol. Assoc. U.K. 58:749-772.

FASHAM, M. J. R.
1978. The statistical and mathematical analysis of plankton patchiness. Oceanogr. Mar. Biol. Annu. Rev. 16:43-79.

FLINT, R. W., AND N. N. RABALAIS (editors).
1981. Environmental studies of a marine ecosystem: South Texas outer continental shelf. Univ. Texas Press, Austin, 240 p.

FOULDS, J. B., AND K. H. MANN.
1978. Cellulose digestion in *Mysis stenolepis* and its ecologic implications. Limnol. Oceanogr. 23:760-766.

GRANT, W. E., AND W. L. GRIFFIN.
1979. A bioeconomic model of the Gulf of Mexico shrimp fishery. Trans. Am. Fish. Soc. 108:1-13.

GUNTER, G.
1962. Shrimp landings and production of the State of Texas for the period 1956-1959, with a comparison with other Gulf states. Publ. Inst. Mar. Sci., Univ. Tex. 8:216-226.

HEEGAARD, P. E.
1953. Observations on spawning and larval history of the shrimp, *Penaeus setiferus* (L.). Publ. Inst. Mar. Sci., Univ. Tex. 3(1):73-105.

HILDEBRAND, H. H., AND G. GUNTER.
1952. Correlation of rainfall with the Texas catch of white shrimp, *Penaeus setiferus* (L.). Publ. Inst. Mar. Sci., Univ. Tex. 3(1):73-105.

HOPKINS, T. L.
1963. The variation in the catch of plankton nets in a system of estuaries. J. Mar. Res. 21:39-47.

INGLIS, A.
1960. Brown shrimp movements. *In* Galveston Biological Laboratory fishery research for the year ending June 30, 1960, p. 66-69. U.S. Fish Wildl. Serv., Circ. 92.

IVERSEN, E. S., AND C. P. IDYLL.
1960. Aspects of the biology of the Tortugas pink shrimp *Penaeus duorarum*. Trans. Am. Fish. Soc. 89:1-8.

KLIMA, E. F.
1964. Mark-recapture experiments with brown and white shrimp in the northern Gulf of Mexico. Proc. Gulf Caribb. Fish. Inst. 16th Annu. Sess., p. 52-64.

KUTKUHN, J. H.
1966. Dynamics of a penaeid shrimp population and management implications. U.S. Fish Wildl. Serv., Fish. Bull. 65:313-338.

LAKSHMI, G. J., A. VENKATARAMIAH, AND G. GUNTER.
1976. Effects of salinity and photoperiod on the burying behavior of brown shrimp *Penaeus aztecus* Ives. Aquaculture 8:327-336.

LIE, U.
1968. A quantitative study of benthic infauna in Puget Sound, Washington, U.S.A. in 1963-1964. Fiskeridir. Skr. Ser. Havunders. 14:229-556.

MARTIN, Q., G. POWELL, G. THORN, G. CHANG, S. BELAIRE, A. GOLDSTEIN, AND G. LANEMAN.
1980. Lavaca-Tres Palacios estuary: a study of the influence of freshwater inflows. Texas Dep. Water Resour. Publ. LP-106.

MCINTYRE, A. D., A. L. S. MUNRO, AND J. H. STEELE.
1970. Energy flow in a sand ecosystem. *In* J. H. Steele (editor), Marine food chains, p. 19-31. Oliver and Boyd, Edinb.

MILLS, E. L.
1975. Benthic organisms and the structure of marine ecosystems. J. Fish. Res. Board Can. 32:1657-1663.

MILLS, E. L., AND R. O. FOURNIER.
1979. Fish production and the marine ecosystems of the Scotian Shelf, eastern Canada. Mar. Biol. (Berl.) 54:101-108.

MORIARTY, D. J. W.
1977. Quantification of carbon, nitrogen, and bacterial biomass in the food of some penaeid prawns. Austr. J. Mar. Freshwater Res. 28:113-118.

NICHOLS, F. H.
1977. Infaunal biomass and production on a mudflat, San Francisco Bay, California. *In* B. C. Coull (editor), Ecology of marine benthos, p. 339-357. Univ. S.C. Press, Columbia.

PÉREZ FARFANTE, I.
1969. Western Atlantic shrimps of the genus *Penaeus*. U.S. Fish Wildl. Serv., Fish. Bull. 67:461-590.

ROWE, G. T., P. T. POLLONI, AND S. G. HORNER.
1974. Benthic biomass estimates from the northwestern Atlantic Ocean and northern Gulf of Mexico. Deep-Sea Res. 21:641-650.

RYTHER, J. H., AND C. S. YENTSCH.
1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. Limnol. Oceanogr. 2:281-286.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry; the principles and practice of statistics in biological research. W. H. Freeman, San Franc., 776 p.

ST. AMANT, L. S., J. G. BROOM, AND T. B. FORD.
1966. Studies of the brown shrimp, *Penaeus aztecus*, in Barataria Bay, Louisiana, 1962-1965. Proc. Gulf Caribb. Fish. Inst. 18th Annu. Sess., p. 1-17.

STEELE, J. H.
1974. The structure of marine ecosystems. Harv. Univ. Press, Camb., Mass., 128 p.

STRICKLAND, J. D. H., AND T. R. PARSONS.
1968. A practical handbook of seawater analysis. Fish. Res. Board Can., Bull. 167, 311 p.

TRENT, L.
1967. Size of brown shrimp and time of emigration from the Galveston Bay system, Texas. Proc. Gulf Caribb. Fish. Inst. 19th Annu. Sess., p. 7-16.

U.S. NATIONAL MARINE FISHERIES SERVICE.
1976. Gulf coast shrimp data, annual summary 1975. U.S. Natl. Mar. Fish. Serv., Curr. Fish. Stat. 6925, 13 p.
1978. Gulf coast shrimp data, annual summary 1976. U.S. Natl. Mar. Fish. Serv., Curr. Fish. Stat. 7225, 13 p.

WIEBE, P. H., AND W. R. HOLLAND.
1968. Plankton patchiness: effects on repeated net tows. Limnol. Oceanogr. 13:315-321.

FEEDING SELECTIVITY OF DOVER SOLE, *MICROSTOMUS PACIFICUS*, OFF OREGON

WENDY L. GABRIEL[1] AND WILLIAM G. PEARCY[2]

ABSTRACT

Factors influencing the selection of food by Dover sole were investigated by analyzing stomach contents of fish and serially sectioned box core samples for benthic invertebrates from two areas of high Dover sole abundance on the central Oregon continental shelf. At both locations (119 and 426 m depth), polychaetes and ophiuroids were more important than molluscs and crustaceans as food in terms of frequency of occurrence, weights, and numbers. Polychaetes and ophiuroids were generally positively selected at both locations; i.e., they were more common in fish stomachs than in box core samples. Molluscs were generally negatively selected at both locations. Crustaceans were positively selected at 426 m and consumed nonselectively at 119 m. The box core samples may, however, underestimate crustaceans and hence give artificially high values of electivity.

Significant changes in frequency of occurrence of principal prey taxa with fish size were observed for 27 principal prey taxa at 119 m and 7 prey taxa at 426 m. These changes indicate that composition of fish diet varies with fish size.

At the 119 m station, the larger the fish size at which a significant difference in prey frequency occurred, the larger the increase in electivity across the size interval. This implies increased selectivity by large fish. Body size of a prey taxon was positively correlated with fish length at which significant difference in prey frequency occurred: larger fish consumed larger prey. Mean depth of a prey taxon within the sediment was also positively correlated with the length of fish at which a significant increase in prey frequency occurred: larger fish consumed prey found deeper in sediment.

Few size-related changes in diet were found at the 426 m location. Environmental abundance of a preferred taxon, polychaetes, was lower at 426 m than at 119 m. Dover sole may therefore change feeding strategy from that of a specialized predator, whose feeding habits vary with its body size where polychaetes are abundant, to that of a generalist consuming more types and sizes where few polychaetes are available. Vertical distribution of prey within the sediment at 426 m was shallower than at 119 m; thus the advantage afforded large fish in removing deeply buried prey may be eliminated. Implications of results are discussed in terms of optimal foraging strategy.

The Dover sole, *Microstomus pacificus*, is a prominent member of the deepwater continental shelf community off Oregon (Pearcy 1978) and makes the largest contribution to total biomass of flatfishes landed commercially off the coast of Oregon (Demory et al.[3]). Yet the published literature on the trophic role of this species in deepwater continental shelf assemblages is sparse. Hagerman (1952) listed "small bivalves...scaphopods ...sipunculids, polychaetes (*Nereis* sp.), nematodes, echinoids (sea urchins), ophiuroids (brittle stars),...gastropods (*Thais* sp.),...at times... shrimp and other crustacean forms" as principal prey animals off California. Pearcy and Hancock (1978) included a list of 35 common polychaete species or taxa, 7 crustacean species or taxa, 9 mollusc species or taxa, and 2 echinoderm taxa consumed by Dover sole collected on the central Oregon continental shelf.

Although selectivity has long been considered an important aspect in resource partitioning within and among species, few studies have included a survey of available food items on which to base and compare feeding habit descriptions of benthic fishes. Early work by Steven (1930) described prey available and consumed by demersal fishes in the English Channel. Later, Jones (1952) related the Cumberland coast bottom fauna and food of flatfishes. More recently, Arntz (1978) described the benthic food web of the western Baltic, including food selection by the two most common demersal fish species found there (the cod, *Gadus*

[1]School of Oceanography, Oregon State University, Corvallis, Oreg.; present address: Fisheries Program, Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, MA 01003.
[2]School of Oceanography, Oregon State University, Corvallis, OR 97331.
[3]Demory, R. L., M. J. Hosie, N. TenEyck, and B. O. Forsberg. 1976. Groundfish surveys on the continental shelf off Oregon, 1971-74. Oreg. Dep. Fish Wildl. Inf. Rep. 76-9, 7 p.

Manuscript accepted June 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

morhua, and the dab, *Limanda limanda*). Levings (1974) investigated seasonal changes in feeding and particle selection by winter flounder, *Pseudopleuronectes americanus*, and Moore and Moore (1976) studied various factors influencing the selection of food by the flounder *Platichthys flesus*. In North Pacific demersal communities, however, even the qualitative aspects of selectivity and the role of selectivity in trophic dynamics have yet to be estimated.

The objectives of this study are to: 1) describe the food habits of the Dover sole in an area of an active commercial fishery for this species off Oregon, 2) determine if the species is a selective feeder, and 3) determine how feeding habits are related to location of fish capture, size of fish, and size and depth of prey in the sediment.

METHODS AND MATERIALS

Samples of demersal fishes and benthic invertebrates were taken on the central continental shelf off Oregon in locations of high Dover sole abundance (Demory et al. footnote 3; Tyler[4]) (Figure 1). Station SG29 (lat. 44°05.0′ N, long. 124°35.0′ W) was located in Heceta Swale, the region east of Heceta Bank. The mean sampling depth was 119 m; the sediment is silty sand (Maloney 1965). Station SG10 (lat. 43°49.3′ N, long. 124°50.0′ W) was located south of Heceta Bank. The mean sampling depth was 426 m. The sediment is glauconitic sand; however, sediment distribution is patchy in this area (Bertrand 1971). Samples were taken over a limited area and time interval to reduce large-scale spatial and temporal variability (SG29: 41.6 km^2, 44 h; SG10: 34.21 km^2, 27 h; day and night 20-24 June 1976).

Benthic infauna was sampled at each station by two box corers: a 0.1 m^2 Bouma box corer (Bouma 1969) and a modified 0.25 m^2 Hessler-USNEL box corer (Hessler and Jumars 1974). The Hessler-USNEL box corer is designed to reduce pressure waves which often blow away small surface invertebrates before corer impact. Box cores provide the largest, deepest, and least disturbed sample of consistent surface area when compared with other commonly used sediment samplers (Word[5]). In <45 min after retrieval of the core, core samples were extruded in 0.1 m^2 boxes and sectioned at 1 cm intervals for the first 10 cm, 2 cm intervals for the next 10 cm, and 4 cm intervals for the remainder of the core. These sections were then washed onto a 1 mm aperture sieve screen, and washed invertebrate samples were preserved in 4% unbuffered formaldehyde.

Beam trawl tows to sample Dover sole were made in the immediate area of box core sampling. A beam trawl with an effective trawling width of 2.72 m (Carey and Heyomoto 1972) and 3.8 cm stretched mesh lined with 1.3 cm mesh netting was towed at 3 kn for 30 min per haul at SG29 and 20 min at SG10. Fish were preserved in 8% (unbuffered) formaldehyde as soon as possible after the trawl was brought aboard. The body cavities of fish >12 cm were slit to allow rapid formaldehyde penetration into the coelom.

A total of four 0.1 m^2 box cores, eight 0.25 m^2 box cores, and 15 successful beam trawl tows were made at SG29. At SG10, nine 0.1 m^2 box cores and 10 successful beam trawl tows were made.

In the laboratory, invertebrates from box cores were transferred to 70% isopropyl alcohol, sorted into major taxa, and identified to species whenever possible. Dover sole were measured (standard length) and stomachs (from esophagus to constriction before pyloric caeca) were removed and transferred to 70% isopropyl alcohol. A total of 202 stomachs from SG29 and 63 stomachs from SG10 were processed. Stomach contents were sorted into phyla and identified to species whenever possible. Total lengths of polychaetes, aplacophorans, and scaphopods were measured. Gastropod and pelecypod measurements were made along the longest axis and included shells. Crustaceans were measured from base of rostrum to point of flexure of abdomen. Since ophiuroids occurred as pieces, a single measurement of ophiuroid volume per stomach was made.

Dry weights of prey items were estimated using conversion factors. Shells, tubes, massive paleal setae (in the case of the polychaete *Pectinaria californiensis*), and posterior scutes (in the case of the polychaete *Sternaspis fossor*) were removed before individual items of known length were dried (36 h, 65° C). Items were weighed using an electrobalance or Mettler[6] balance. Regression curves were fitted to sets of length-weight points

[4]A. V. Tyler, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, pers. commun. June 1976.

[5]Word, J. Q. 1977. An evaluation of benthic invertebrate sampling devices for investigating feeding habits of fish. *In* C. A. Simenstad and S. J. Lipovsky (editors), Proc. 1st Pac. NW. Tech. Workshop. Fish food habits studies, p. 43-55. Washington Sea Grant, Seattle. WSG-WO-77-2.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

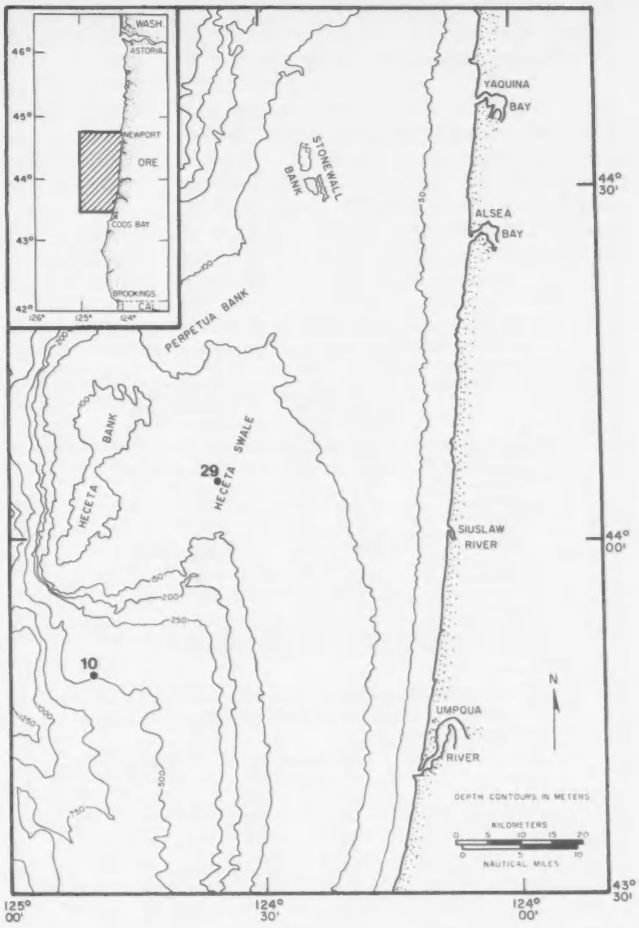

FIGURE 1.—Location of sampling stations on the central continental shelf off Oregon.

for gastropods, pelecypods, amphipods, cumaceans, and "noncylindrical" polychaetes (*Sternaspis fossor*); otherwise, a simple milligram per centimeter conversion factor was calculated for polychaetes, aplacophorans, and scaphopods. For each prey taxon, at least 10% of the total number consumed or 20 individuals were dried and weighed. Although formaldehyde and particularly alcohol are known to leach organic material from biological specimens and to reduce the weight of the organisms (Thorson 1957; Howmiller 1972), these estimates were assumed to be adequate for estimating relative importance of prey taxa biomass. Dry weights of ophiuroids overestimate the food value of these animals compared with soft-bodied polychaetes. Therefore, ash-free dry weight estimations were made for all groups from conversion factors found in the literature and previous laboratory work for shell-free or tube-free weights (Richardson et al.[7]; Ruff[8]).

[7]Richardson, M. D., A. G. Carey, Jr., and W. H. Colgate. 1977. The effects of dredged material disposed on benthic assemblages off the mouth of the Columbia River. *In* Final report, Department of the Army Corps of Engineers, p. 59. Contracts DACW 57-75-C0137 and DACW 57-76-C-0092.

[8]R. E. Ruff, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. March 1978.

RESULTS

Feeding Habits of Dover Sole

Dover sole off the Oregon coast in midsummer fed most often on polychaetes, although a surprisingly large proportion of the diet consisted of ophiuroids (Table 1). At station SG29, polychaetes occurred in 97.3% of stomachs examined, and composed 43% of the total ash-free dry weight of stomach contents examined. Ophiuroids occurred in 63.0% of the stomachs, made up 41% of the ash-free dry weight of stomach contents at that location. At station SG10, polychaetes occurred in 83.6% of the stomachs examined and constituted 11% of total ash-free dry weight of stomach contents examined, while ophiuroids occurred in 80% of those stomachs, composing 84% of ash-free dry weight of the diet at SG10; otherwise, crustaceans and molluscs made up <6% of biomass consumed.

The largest proportion of polychaete biomass consumed was derived from *Pectinaria californiensis* and members of the families Glyceridae (SG29: *Glycera capitata*, SG10: *Glycinde picta*),

TABLE 1.—Percentage of frequency of occurrence, numerical abundance, dry weight, and ash-free dry weight that polychaetes, molluscs, crustaceans, and ophiuroids composed in Dover sole stomachs at SG29 and SG10.

	Percent frequency of occurrence		Percentage of numerical total[1]		Percentage of total dry weight		Percentage of total ash-free dry weight	
Taxon	SG29	SG10	SG29	SG10	SG29	SG10	SG29	SG10
Polychaeta	97.3	83.6	84.7	57.7	22.3	3.6	42.7	10.5
Mollusca	68.6	69.1	9.1	15.4	6.0	1.0	14.5	3.5
Gastropoda	8.0	20.0	.4	2.3	.3	.3		
Pelecypoda	61.2	50.9	7.2	9.9	5.2	.5		
Scaphopoda	12.2	16.4	.7	1.5	.3	.1		
Aplacaphora	16.9	14.5	.7	1.7	.2	.1		
Crustacea	62.2	83.6	6.2	26.9	.9	.8	1.5	2.1
Miscellaneous[2]	15.3	18.2	.7	2.0	.5	.2		
Cumacea	26.6	47.3	1.5	5.5	.1	.2		
Amphipoda	48.9	76.4	3.9	19.4	.3	.4		
Ophiuroidea	63.0	80.0			70.8	94.6	41.4	84.0

[1]Ophiuroids excluded from total, since this organism was nearly always found as uncountable fragments of arms.
[2]Includes Ostracoda, Copepoda, Pericarida, and Eucarida.

TABLE 2.—Frequency of occurrence of polychaete families in Dover sole, and percentage composition of polychaetes found in stomachs on numerical and dry weight bases at SG29 and SG10.

	Percent frequency of occurrence		Percentage of numerical total of polychaetes		Percentage of total dry weight of polychaetes	
Family	SG29	SG10	SG29	SG10	SG29	SG10
Ampharetidae	19.1	34.5	2.0	8.5	1.5	2.5
Apistobranchidae	18.1	1.8	1.3	.2	.1	.1
Arenicolidae	.5	0	.1	0	<.1	.1
Capitellidae	52.7	30.9	7.7	7.6	1.8	1.7
Chaetopteridae	2.7	0	<.1	0	<.1	0
Cirratulidae	26.1	18.2	2.1	5.0	.6	1.6
Cossuridae	33.5	0	4.4	0	.2	0
Flabelligeridae	5.9	3.6	.4	.9	3.6	2.4
Glyceridae	43.6	18.2	3.7	4.0	11.3	14.1
Goniadidae	3.2	14.5	.2	1.2	.8	6.5
Lumbrineridae	81.4	23.6	19.2	4.3	4.5	1.6
Magelonidae	6.4	5.5	.3	.7	.4	1.0
Maldanidae	39.9	21.8	4.3	4.0	4.5	3.2
Nephtyidae	34.6	60.0	3.4	24.6	.5	2.8
Nereidae	1.1	0	<.1	0	<.1	0
Onuphidae	13.8	3.6	.9	.7	3.7	.5
Opheliidae	1.6	25.5	<.1	5.2	.5	7.4
Orbiniidae	4.3	0.0	.2	0	<.1	0
Oweniidae	56.9	14.5	8.8	1.7	.8	.1
Paraonidae	78.7	45.5	24.1	14.7	4.0	5.5
Pectinaridae	11.7	18.2	1.1	3.1	20.9	29.2
Phyllodocidae	17.0	7.3	1.1	2.8	.1	.6
Polynoidae	.5	0	<.1	0	<.1	0
Sabellidae	.5	3.6	<.1	.5	<.1	.1
Sigalionidae	23.9	29.1	1.6	4.0	.3	2.6
Sphaerodoridae	.5	0	<.1	0	<.1	0
Spionidae	51.6	9.1	5.9	1.4	4.7	1.4
Sternaspidae	32.4	5.5	2.1	.9	12.1	4.5
Syllidae	6.9	7.3	.3	.7	<.1	0
Terebellidae	31.9	16.4	3.8	3.1	22.7	10.5

Terebellidae (SG29: *Pista disjuncta*), Sternaspidae (SG29: *Sternaspis fossor*), and Opheliidae (SG10: *Travisia foetida*). Most frequently consumed polychaete species were generally smaller bodied, including lumbrinerid (primarily at SG29), nephtyd (primarily at SG10), paraonid, and capitellid polychaetes (Table 2). Principal prey species are listed in Tables 3 (SG29) and 4 (SG10).

Pelecypods were the most frequently consumed molluscs, constituting most of the mollusc biomass eaten (Table 1). *Macoma* spp., *Adontorhina cyclia*, and *Axinopsida serricata* were most important at SG29 and *Crenella decussata, Huxleyia munita*, and *Odontogena borealis* were common at SG10. Among crustaceans, amphipods (SG29: *Harpiniopsis excavata, H. fulgens*; SG10: *Melphidippa amorita, Ampelisca macrocephala, Nicipe tumida*) occurred more frequently and in larger numbers than cumaceans, and were consumed more often than molluscs at the deeper station.

Changes in Diet with Predator Length

A chi-square test (Tyler[9]) was used to determine the dependency of diet on fish size, based on differences in frequency of occurrence of prey items consumed by predators belonging to different length intervals. The chi-square test showed many size-related variations in the diet of Dover sole taken at SG29 but few in the diet at SG10. At

[9]Tyler, A. V. 1969. Computer programs for analysis of feeding heterogeneities related to predator body size. Fish. Res. Board Can. Tech. Rep. 121, 49 p.

TABLE 3.—SG29: Changes in selectivity with fish size considered by principal prey taxa. Range of fish size is divided to maximize heterogeneity between size intervals for each principal prey taxon as described in text.

	Taxon	For fish <length (cm)	Ivlev index of electivity	Chi-square value	Significance[1]	For fish ≥length (cm)	Ivlev index of electivity	Chi-square value	Significance[1]
1	Polychaeta:								
2	Ampharetidae[2]	31	0.45	8.646	***	31	−0.33	2.060	NS
3	Apistobranchidae: *Apistobranchus ornatus*	21	−1.00	.568	NS	21	.59	7.286	**
4	Capitellidae: *Decamastus gracilis*	29	−.05	1.957	NS	29	.15	2.086	NS
5	Cirratulidae: *Tharyx* spp.[3]					11	−.13	3.034	NS
6	Cossuridae: *Cossura* sp.	29	.52	11.762	***	29	.72	42.421	***
7	Glyceridae: *Glycera capitata*	37	−.12	1.781	NS	37	.55	18.297	***
8	*Glycinde picta*					11	.69	11.073	***
9	Lumbrineridae: *Lumbrineris latreilli*					11	.68	149.112	***
10	*Ninoe gemmea*	32	−.76	33.946	***	32	−.20	1.858	NS
11	Maldanidae[2]	33	−.64	206.469	***	33	−.18	12.331	***
12	Nephtyidae: *Nephtys* sp.	33	.67	25.046	***	33	.54	7.781	**
13	Onuphidae: *Nothria* spp.[4]	35	−.62	17.607	***	35	.50	10.411	***
14	Oweniidae: *Myriochele heeri*	33	.15	.540	NS	33	−.48	5.548	*
15	*M. oculata*	33	−.17	17.364	***	33	−.60	37.979	***
16	Paraonidae[2]	21	.42	15.575	***	21	.60	179.784	***
17	*Aedicira antennata*[5]	24							
18	*Aricidea ramosa*	21	.66	22.164	***	21	.73	86.711	***
19	*Paraonis gracilis*[5]	21							
20	Pectinaridae: *Pectinaria californiensis*	34	−.38	.851	NS	34	.91	59.486	***
21	Phyllodocidae: *Anaitides groenlandica*[6]	29	.08	.127	NS	29	.66	5.983	*
22	Sigalionidae[2]	24	.77	2.343	NS	24	.93	21.043	***
23	Spionidae: *Prionospio* spp.[3]					11	.12	.144	NS
24	*Spiophanes* spp.[3]	26	−.35	9.185	***	26	.08	.129	NS
25	*S. berkeleyorum*	27	−.47	17.738	***	27	−.19	5.501	*
26	Sternaspidae: *Sternaspis fossor*	21	−1.00	2.775	NS	21	.22	1.613	NS
27	Terebellidae: *Pista cristata*	35	.19	0.625	NS	35	.79	66.159	***
28	*Terebellides stroemii*	28	−.70	13.772	***	28	−.13	1.180	NS
	Mollusca:								
29	Pelecypoda (unidentifiable, nonprincipal)[7]					11	−.81	668.332	***
30	"A-type"[8]	33	−.55	195.445	***	33	−.95	137.863	***
31	*Macoma* spp.[3]					11	−.47	50.222	***
32	Scaphopoda	28	−.86	80.797	***	28	−.68	70.064	***
33	Aplacophora					11	.09	.002	NS
	Crustacea:								
34	Cumacea: *Eudorella pacifica*	35	−.07	.859	NS	35	−.72	8.243	***
35	Amphipoda: *Harpiniopsis excavata*[9]					11			
36	*H. fulgens*[9]	36	.38	6.935	**	36	−.01	.001	NS
37	Ophiuroidea[10]	28	.92	37.430	***	28	.93	41.757	***

[1]NS = not significant; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.
[2]All members of family pooled.
[3]All members of genus pooled (species identifications not possible).
[4]Members of two species pooled based on taxonomic uncertainty (*Nothria elegans* and *N. iridescens*).
[5]No members of this genus present in box core.
[6]All members of genus pooled (species identifications tentative or uncertain).
[7]All nonprincipal or unidentifiable pelecypods found in fish compared with all pelecypods found in box core.
[8]*Axinopsida serricata* and *Adontorhina cyclia* pooled.
[9]No members of this genus present in box cores, value for *Harpiniopsis fulgens* represents all Phoxocephalidae, pooled.
[10]Based on frequency of occurrence in fish compared with numbers of ophiuroids found in box core.

TABLE 4.—SG10: Changes in selectivity with fish size considered by principal prey taxon. Range of fish size is divided to maximize heterogeneity between size intervals for each principal prey taxon as described in text.

Taxon	For fish >length (cm)	Ivlev index of electivity	Chi-square value	Significance[1]
Polychaeta:				
Ampharetidae[2]	24	0.57	11.875	***
Capitellidae: *Decamastus gracilis*[3]	24	−.22	4.777	*
Cirratulidae: *Tharyx* sp.[4]	24	.89	11.436	***
Glyceridae: *Glycinde* sp.	28	.59	3.320	NS
Lumbrineridae: *Lumbrineris* sp.[4]	24	.77	8.518	***
Maldanidae[2]	24	−.32	5.788	*
Nephtyidae: *Nephtys* sp.	24	.98	91.741	***
Opheliidae: *Travisia* sp.[4]	24	.91	15.763	***
Paraonidae[2]	24	.45	13.691	***
Pectinaridae: *Pectinaria californiensis*[5]	24	.41	1.823	NS
Sigalionidae[2]	24	.68	6.778	**
Mollusca:				
Pelecypoda (unidentifiable, nonprincipal)	24	−.35	14.176	***
Huxleyia munita	24	−.84	110.067	***
Crenella decussata	24	−.78	171.609	***
Odontogena borealis	25	−.81	61.853	***
Gastropoda: pteropoda[6]	24			
Scaphopoda	24	−.39	5.516	*
Aplacophora	26	.28	.756	NS
Crustacea:				
Amphipoda: *Melphidippa amorita*[6]				
Nicipe tumida[6]				
Metopa sp.				
Ampelisca macrocephala	24	.77	8.518	***
Cumacea: *Campylaspis* sp.[4]	24	.79	14.800	***
Ophiuroidea[7]	24	.25	3.764	NS

[1]NS = not significant; ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.
[2]All members of the same family pooled.
[3]Positive identification of species difficult for this species, pooled with *Mediomastus californiensis*.
[4]Species not found in box core, calculation based on numbers of representatives of same genus.
[5]Species pooled with *Pectinaria belgica*.
[6]No representative of genus in box core—no electivity values calculated.
[7]Based on frequency of occurrence in fish compared with numbers of ophiuroids found in box core.

SG29, out of 35 principal prey taxa (taxa occurring in at least 10% of stomachs containing food), 27 showed significant changes in frequency of occurrence. Five types of prey frequency patterns were apparent for these 27 prey over the size range of fish sampled, 11-42 cm. Examples are shown in Figure 2.

The first prey pattern, typified by the polychaete *Decamastus gracilis* (I), reflects prey which occurred at low frequencies in diets of small-sized fish (11-20 cm) and at increasing frequency in diets in intermediate-sized fish (21-30 cm), and which remained approximately constant at that same frequency in the diets of large-sized fish (30-42 cm) (Figure 2). Other taxa for which this pattern existed include the Ophiuroidea; polychaetes *Aedicira antennata, Spiophanes berkeleyorum*, the Sigalionidae, *Ninoe gemmea, Spiophanes* sp.; and the Scaphopoda, many of which are sessile or motile outside of tubes and surface feeders.

The second prey pattern describes taxa which occurred at relatively high frequency in diets of small-sized fish and occurred at decreased frequency in diets of intermediate- and large-sized fish; e.g., the small tubed polychaetes *Myriochele oculata* (II) and *M. heeri*, the amphipod *Harpiniopsis fulgens*, and small ampharetid polychaetes. The cumacean *Eudorella pacifica*, pelecypod group *Adontorhina cyclia-Axinopsida serricata*, and polychaete *Nephtys* sp. also occurred often in diets of intermediate-sized fish, but occurred at low frequency in diets of large-sized fish.

The third prey pattern is depicted by a hump-shaped curve, in which case a prey taxon occurred at low frequencies in diets of small- and large-sized fish but at relatively high frequencies in diets of intermediate-sized fish. Many principal prey taxa belong to this category, including the polychaetes *Anaitides groenlandica* (III), *Aricidea ramosa, Sternaspis fossor, Paraonis gracilis, Apistobranchus ornatus, Cossura* sp., and *Terebellides stroemii*.

The fourth prey pattern reflects increasing prey frequency with increasing fish size. Prey taxa following this pattern included many larger tubed, surface and subsurface feeding polychaetes: *Nothria elegans* (IV), *Pectinaria californiensis, Glycera capitata, Pista cristata*, and the Maldanidae.

The fifth prey pattern includes prey whose frequency of occurrence in diets did not change significantly over the entire size range of fish sampled; e.g., polychaetes *Lumbrineris latreilli* (V),

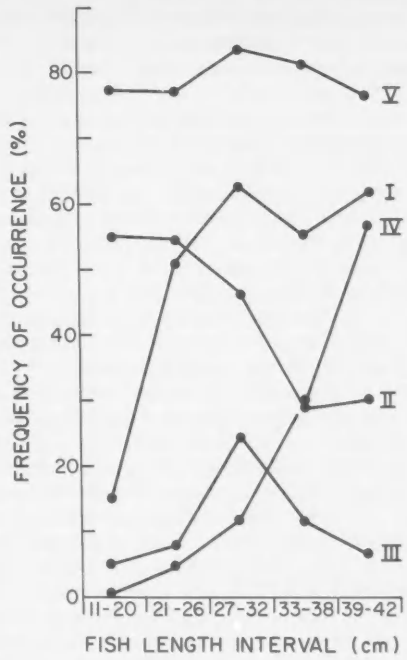

FIGURE 2.—Five patterns of change in the frequency of occurrence of prey for different sizes of Dover sole at SG29. Curve shape I typified by *Decamastus gracilis*, shape II by *Myriochele oculata*, shape III by *Anaitides groenlandica*, and shape IV by *Nothria elegans*.

Glycinde picta, *Prionospio* sp., *Tharyx* sp., the amphipod *Harpiniopsis excavata*, the Aplacophora, unidentifiable Pelecypoda, and *Macoma* sp.

At SG10, 19 out of the 26 principal prey species showed no significant change in frequency of occurrence over the range of fish sampled (24-43 cm). The frequency of occurrence of *Melphidippa amorita*, an amphipod, increased significantly in fishes 32 cm or longer. Occurrence of two amphipod taxa, *Nicipe tumida* and *Metopa* sp., decreased significantly in fish 32-33 cm or larger. In the case of the four remaining taxa, the series of chi-square tests produced intervals across which frequency of occurrence changed gradually, rather than defining a well-marked break in frequency at one particular length. *Glycinde picta*, a tubeless, subsurface deposit feeding polychaete, increased in frequency in fish 28-29 cm or longer. *Odontogena borealis*, a small bivalve, increased over the 25-32 cm fish size interval. Aplacophorans increased in frequency in 26-27 cm fish and longer, and Ophiuroidea increased in the 30-32 cm interval.

Selectivity

A chi-square test of 2×2 contingency tables was used to test the null hypothesis that the relative abundance of a taxon among items consumed is dependent on the relative abundance of the taxon in the environment. Ivlev's (1961) index of electivity

$$E = (r_i - p_i)/(r_i + p_i),$$

where r_i = percentage of ration composed of a given prey taxon i and p_i = percentage of food complex in environment composed of prey taxon i, was used to determine whether selection was positive or negative. Overall trends in selectivity by major taxa for all fish from each station are shown in Table 5. Ophiuroids were the most highly selected food taxon at SG29. The calculations of electivity indices and chi-square values for this taxon were based on number of occurrences rather than number of individuals consumed, and hence underestimated the importance of ophiuroids. Ophiuroids were removed from the data sets for subsequent calculations so that estimations for other taxa were unbiased by this representation. Polychaetes were selected food of fish at both locations. Chi-square values were larger for polychaetes than any other positively selected taxon. Molluscs, especially pelecypods and

TABLE 5.—Summary of selectivity considered by major taxa at stations SG29 and SG10 for Dover sole of all sizes.

Station	Taxon	Ivlev index of electivity	Chi-square value	Significance[1]
SG29	Polychaeta	0.13	243.451	***
	Mollusca:			
	Pelecypoda	−.49	248.739	***
	Gastropoda	−.43	6.015	**
	Scaphopoda	−.75	112.448	***
	Aplacophora	.09	.105	NS
	Crustacea:			
	Amphipoda	.08	.839	NS
	Cumacea	−.10	.766	NS
	Ophiuroidea	.92	40.724	***
SG10	Polychaeta	.33	117.446	***
	Mollusca:			
	Pelecypoda	−.72	425.683	***
	Gastropoda	.50	4.061	*
	Scaphopoda	−.39	4.602	*
	Aplacophora	.28	1.039	NS
	Crustacea:			
	Amphipoda	.69	79.629	***
	Cumacea	.67	20.771	***
	Ophiuroidea	.25	3.764	NS

[1]NS = not significant; ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.

scaphopods, were the least often selected food at both locations. Aplacophoran molluscs, however, were neither significantly selected nor rejected. At SG29, the numerical proportions of crustaceans (amphipods and cumaceans) in stomachs and box core samples were nearly equal. At SG10, however, these crustaceans appeared highly selected.

Among polychaetes at SG29, the most highly selected prey species were *Glycinde picta* and *Lumbrineris latreilli* (in fish of all sizes, i.e., >11 cm), Sigalionidae (especially in fish >21 cm), *Aricidea ramosa* (in fish of all sizes, but especially those >21 cm), *Cossura* sp. (in fish of all sizes, but especially those >29 cm), *Pectinaria californiensis* (in fish >34 cm), and *Pista cristata* (in fish >35 cm) (Table 3). No principal mollusc taxa were selected, with the exception of aplacophorans, which appeared to be neither significantly selected nor ignored. The cumacean *Eudorella pacifica* was negatively selected by fish >34 cm. The phoxocephalid amphipod species *Harpiniopsis excavata* and *H. fulgens* were not present in box cores, indicating high selectivity by fish or inadequate box core sampling. If values for all phoxocephalids were pooled, it appeared that the family was selected positively by fish <36 cm.

Changes in electivity related to fish size and prey taxa are shown in Figure 3. Values of E were calculated for each principal prey taxon found at SG29 within three fish size intervals (11-21, 22-31, and 32-42 cm). The patterns of changes in electivity with fish size are similar to the patterns found for changes in frequency of occurrence of prey with fish size in Figure 2. In one pattern, electivity of a prey taxon was low by small fish, higher by intermediate fish, and remained constant by large fish relative to intermediate values (Figure 3A). Taxa belonging to this category included the polychaetes *Anaitides groenlandica* (21), *Sternaspis fossor* (26), *Prionospio* spp. (23), *Spiophanes* spp. (24), and *Terebellides stroemii* (28); and the Scaphopoda (32). In the second pattern (Figure 3B), electivity of prey taxa decreased with fish size. Taxa in this category included the polychaetes *Myriochele oculata* (15), *M. heeri* (14), and Ampharetidae (2); phoxocephalid amphipods; the cumacean *Eudorella pacifica* (34); and the combined pelecypod group *Adontorhina cyclia-Axinopsida serricata* (30). In the third category (Figure 3C), electivity was highest by intermediate-sized fish, and lower for larger and smaller fish. Taxa following this pattern included the polychaetes *Cossura* sp. (6), *Tharyx* sp. (5), and *Apistobranchus ornatus* (3). In the fourth

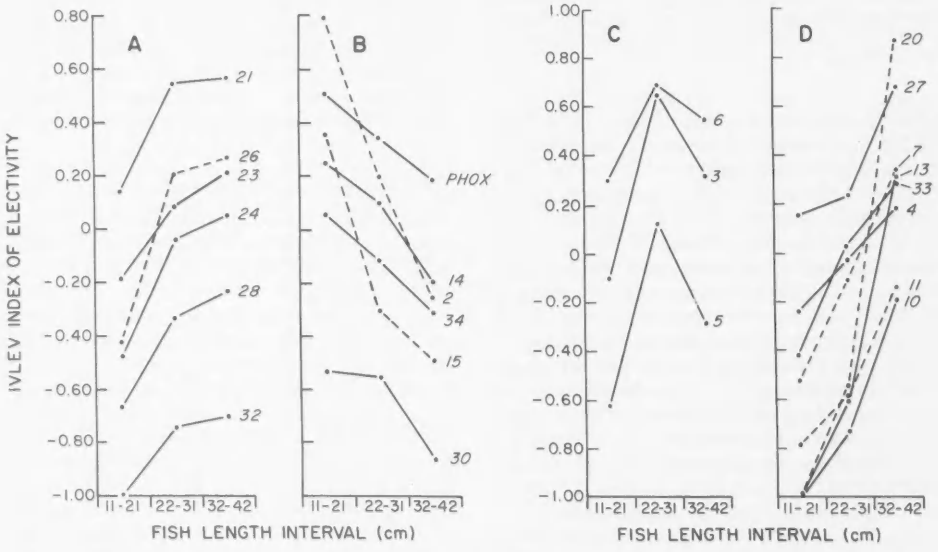

FIGURE 3.—Changes in Ivlev indices of electivity with fish length at SG29. Numbers designate taxa of prey in Table 3. Phox = Phoxocephalidae. Taxa with similar patterns of change are grouped as Figures A, B, C, and D.

category (Figure 3D), electivity increased among all three size categories of fish. This pattern existed for the large-bodied, tubed polychaetes *Pectinaria californiensis* (20), *Pista cristata* (27), *Nothria* sp. (13), and Maldanidae (11), the large-bodied, tubeless polychaete *Glycera capitata* (7); two small-bodied, tubeless polychaetes *Decamastus gracilis* (4) and *Ninoe gemmea* (10); and the aplacophoran molluscs (33). In a fifth pattern (not shown), electivity of a prey taxon did not change significantly with fish size. The polychaetes *Lumbrineris latreilli*, *Glycinde picta*, the Paraonidae, and the Sigalionidae followed this pattern, as did the molluscan genus *Macoma*. Taxa belonging to each category of electivity patterns were not necessarily identical to taxa belonging to each analogous category of frequency of occurrence patterns, since the index of electivity of a prey taxon was based on proportion of numerical abundances of the prey taxon in the diet, rather than on frequency of occurrence.

Among polychaetes at SG10, the most highly selected prey taxa were *Nephtys* sp. and *Tharyx* sp. by fish of all sizes (Table 4). No specimens of *Travisia foetida* or *Lumbrineris latreilli* were found in the core samples so the values shown in Table 4 were based on pooling of the taxa at the generic level. Once again, all principal molluscan taxa were negatively selected, with the exception of aplacophorans (no significant selection) and pteropods, which were not found in core samples. If values for all cumaceans of genus *Campylaspis* were pooled, the taxon appeared positively selected; however, no species common to both fish and box core were found. In the case of amphipods, three of the four principal taxa were not represented in box core samples. The fourth, *Ampelisca macrocephala*, appeared positively selected based on these samples.

Merely because a taxon is positively selected does not mean it plays an especially important role in diet. For example, frequency of occurrence, biomass contribution, and numerical abundance of gastropods in diets of fish at SG10 were small compared with other taxa. Yet this taxon was positively selected (Table 5). Conversely, even though a taxon is negatively selected, it may still play an important role in diets. Positive selection may also be an artifact of the environmental sampling device. Crustaceans appear highly selected at SG10 (Table 5), but this may be partly due to the inefficiency of the box corer in sampling motile epifauna relative to infauna.

A significant positive correlation was found between prey size (weight/length) of 16 prey and the length of fish at which that prey began to significantly increase in frequency ($r = 0.540$, $P < 0.05$) (Figure 4). Large prey were consumed by large fish. Prey which decreased in frequency were generally small-bodied polychaetes (Ampharetidae, *Nephtys* sp., *Myriochele heeri*, *M. oculata*), amphipods, and cumaceans. In the case of the five prey taxa which showed no significant change in frequency in fish of different sizes (Aplacophora, *Glycinde picta*, *Prionospio* sp., *Tharyx* sp., and *Lumbrineris latreilli*) some other criteria for inclusion in diet may have been more important than size.

When prey frequency increased with increased size of Dover sole at SG29, predator selectivity also appeared to increase. From the iterative chi-square tests described earlier, a fish length was found which divided the total fish size range into (usually) two length intervals of statistically homogeneous prey frequency for each prey taxon. A value of E was calculated for each interval, and the difference in values between the two intervals was determined for each applicable prey taxon. This difference was then plotted against the fish

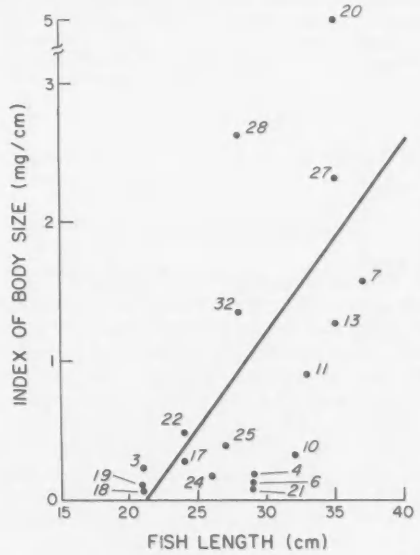

FIGURE 4.—Body size of prey vs. fish length at which frequency of prey increased significantly. Numbers designate prey taxa (see Table 3).

length which separated the two intervals of statistical homogeneity for that prey. (Prey species which were not present over the entire range of fish sampled were not included, e.g., *Apistobranchus ornatus* and *Sternapis fossor*.) For example, the value of E for the polychaete *Glycera capitata* for fish <37 cm was −0.12. For fish 37 cm or larger, the value of E rose to 0.55; the difference, 0.67, was associated with a division point of 37 cm. Although the resulting relationship (Figure 5) may not be amenable to tests of statistical significance, a positive trend exists. Prey which showed an increase in frequency in larger fishes also showed a greater increase in electivity by these larger fish.

Nonparametric ranking statistics were used to test the possible effects of prey mobility, feeding method, and protective structures (polychaete tubes) on size-related increases in prey frequency. The rank for each prey was determined by the fish length at which the prey showed a significant increase in frequency (Table 3). For each test, prey were assigned to categories based on characteristics as described in published literature (Barnes 1968; Smith and Carlton 1975; Jumars and Fauchald 1977) or as described by workers familiar with local fauna (Jones et al.[10]). A lack of difference between summed ranks for each category would imply that the distributions of different prey types (motile, discretely motile, or sessile, in this example) were the same over all fish sizes at which any prey frequency increased; e.g., a prey taxon which was found at higher frequency in fish >21 cm was just as likely to be motile or sessile as one which was found at higher frequencies in fish 35 cm or longer.

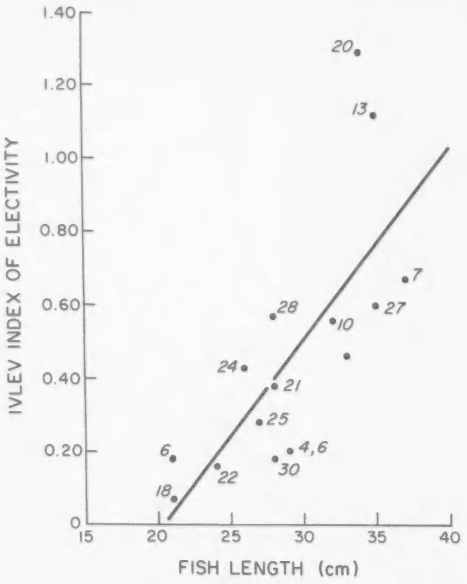

FIGURE 5.—Increase in the Ivlev electivity of prey vs. length of fish at which frequency of that prey increased significantly. Numbers designate prey taxa (see Table 3).

The results of these nonparametric tests (Table 6) show that no one motility type predominated in prey taxa frequent in either small or large fish sizes. Feeding locale, a possible indicator of exposure of a taxon to predation at the sediment surface, was not significant in explaining size-related variations in prey frequency. Feeding type, which is related to both degree of exposure and motility, also showed no trend when ranked over fish lengths. The only statistically significant relationship appeared when ranks for 11 tubed polychaetes were compared with ranks for 7 untubed polychaetes. Tubed taxa generally had a higher rank than untubed taxa. This implied that large fish selected tubed more often than untubed polychaetes. However, three of the four polychaete taxa which decreased in frequency in larger fish (Table 3) have tubes. Thus, the presence or absence of tubes in polychaetes did not always appear to be an important criterion for variation in prey frequency with fish size.

[10]H. Jones, G. Bilyard, and K. Jefferts, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. March 1978.

TABLE 6.—Results of nonparametric tests of effects of prey characteristics on fish size related increases of prey frequency. Prey are ranked by fish size at which prey frequency increased.

Test and categories	Value of test statistic	Critical value for significance[1]
Prey motility:		
Motile	[2]H = 0.029	χ^2 = 5.991
Discretely motile	NS	df = 2
Sessile		
Feeding mechanism:		
Tentaculate	[2]H = 3.508	χ^2 = 5.991
Burrowing (deposit feeder)	NS	df = 2
Carnivorous (raptorial)		
Protective structures:		
Tubed polychaetes	[3]U_S = 58	U_S = 58
Untubed polychaetes	*1	n_1 = 11, n_2 = 7
Feeding locale:		
Surface	[3]U_S = 57	U_S = 72
Subsurface	NS	n_1 = 11, n_2 = 9

[1]Significant at 95% confidence level.
[2]H: result from Kruskal-Wallis test (3 categories) (Sokal and Rohlf 1969).
[3]U_S: result from Wilcoxson two sample test (2 categories) (Sokal and Rohlf 1969).

The mean depth of a prey taxon within the sediment was significantly related to fish size at which frequency of that prey increased (Figure 6, $r = 0.542$, $P < 0.05$). Prey which were important to large fish were usually found deeper in the sediment. Prey occurring frequently in small fish were found near the sediment surface. Prey which occurred at statistically equal frequencies for all-sized fish were generally found within the top 4 cm of the core sample, e.g., *Lumbrineris latreilli*, which was consumed in large numbers by fish of all sizes. Prey which decreased in occurrence in larger fish were often concentrated near the surface, with a mean depth distribution of 2 cm. Although the relationship between depth of prey in sediment and index of body prey was not significant (Figure 7) ($r = 0.220$), few large-bodied principal prey taxa had a mean depth in the sediment <4 cm.

At SG10, few prey taxa changed significantly in frequency of occurrence over the range of fish sizes sampled. The mean depth of a taxon within the sediment was rarely >4 cm, and usually <3 cm, regardless of prey body size. The depth range of all invertebrates at this station was generally shallower than at SG29.

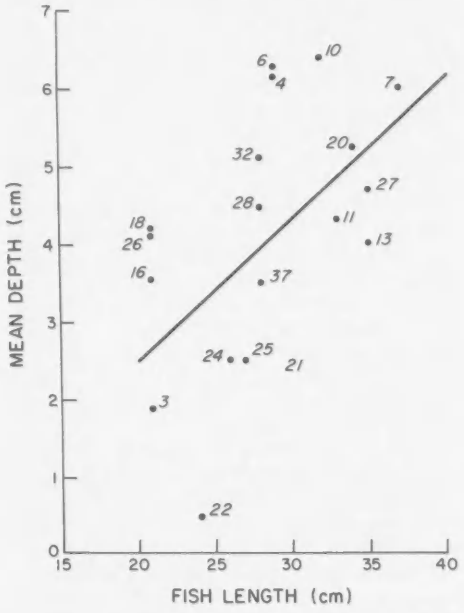

FIGURE 6.—Mean depth of prey in the sediment vs. fish length at which frequency of prey increased significantly. Numbers designate prey taxa (see Table 3).

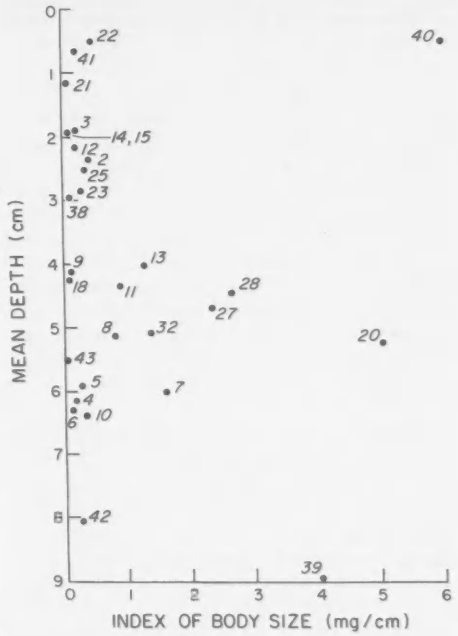

FIGURE 7.—Mean depth of prey in the sediment vs. index of prey body size. Numbers designate prey taxa (see Table 3. Nonprincipal prey: 38 = *Aricidea neosuecica*, 39 = *Laonice cirrata*, 40 = *Pherusa papillata*, 41 = *Polydora socialis*, 42 = *Spiochaetopterus costarum*, 43 = *Haploscoloplos elongatus*).

Prey Abundance Patterns

Prey abundance also varied with location. Although the total density of individuals per square meter was slightly higher at SG10 than SG29, the density of polychaetes, a preferred taxon, averaged 886 individuals/m^2 at SG29 and only 397 individuals/m^2 at SG10 (Table 7). Most principal polychaete taxa were found in lower densities at SG10 than SG29. The density of pelecypod molluscs, a negatively selected (avoided) taxon, was several times higher at SG10 than SG29, 861 and 297 individuals/m^2, respectively.

DISCUSSION

How similar is the Dover sole to the hypothetical

TABLE 7.—Major taxon composition of 19 box core[1] samples containing 154 species taken at SG29 (119 m deep) and 8 box core samples containing 97 species taken at SG10 (426 m deep).

Taxon	SG29		SG10		Bertrand 1971[2]
	No./m²	Percent	No./m²	Percent	
Polychaetes	*886.4*	*65.5*	*396.8*	*26.9*	30.1%
Molluscs	*388.5*	*28.7*	*928.5*	*62.9*	
Pelecypods	296.6	21.9	861.1	58.3	59.2%
Gastropods	14.2	1.0	7.9	.5	1.2%
Scaphopods	66.0	4.9	45.6	3.1	1.2%
Aplacophorans	8.4	10.6	13.9	.9	0%
Other	3.3	.2			
Crustacea	*73.5*	*5.4*	*61.5*	*4.2*	4.4%
Amphipods	45.9	3.4	45.6	3.1	
Cumaceans	25.9	1.9	15.9	1.1	
Other	1.7	.1			
Echinoderms	.8	<.1	*51.6*	*3.5*	2.3%
Ophiuroids	.8	<.1	47.6	3.2	
Miscellaneous	3.3	.2	9.6	2.0	.9%
Individuals	1,352.5	n = 1,619	1,476.2	n = 744	343

[1]Effective sampling area is 0.063 m².
[2]Values found for the same location.

optimal forager that 1) prefers more profitable prey, i.e., prey whose ratio of food value to predator search and handling time is highest, 2) feeds more selectively when profitable prey are common, and 3) ignores unprofitable prey whose addition to the diet lowers the net energy intake per time spent searching and handling (Pyke et al. 1977; Krebs 1978)?

The Dover sole is not a simple opportunistic feeder, consuming all available prey in proportion to their occurrence in the environment. Since the percentage contribution of a major taxon in the diet and in the environment (as reflected by box core samples) was often significantly different, the Dover sole can be termed a selective feeder. For example, polychaetes and ophiuroids played a more important role in the diet than molluscs and crustaceans, despite the fact that polychaetes and ophiuroids were not always most abundant in box core samples. Moreover, trends in selectivity of major taxa were qualitatively similar at both locations despite different abundances of prey. Polychaetes and ophiuroids were always positively selected, occurring more often in the diet than in the environment. Even though density of pelecypod molluscs at SG10 was three times greater than at SG29, the contribution of molluscs to total diet was lower at SG10 than SG29. This general consistency of diet between these two locations in the face of varying abundances of prey, species composition, depth of benthic macrofauna within the sediment, and depth of the station itself does not support a hypothesis of the Dover sole as a simple opportunistic feeder.

The most profitable prey for a Dover sole in terms of food value (gram-calorie per gram dry weight) are first, molluscs and crustaceans; second, polychaetes; and third, ophiuroids (Brawn et al. 1968; Cummins and Wuycheck 1971; Tyler 1973). However, most observations of calories per gram dry weight were made for shell-free molluscs while polychaete weights included tubes. This is probably why values for *Lumbrineris fragilis*, an untubed polychaete, are comparable with those for pelecypods (= 4,500 g cal/g dry weight) and greater than those for amphipods (e.g., 4,050 g cal/g dry weight), while those for tubed polychaetes (e.g., *Pherusa plumosa, Pectinaria hyperborea*) are lower (2,200-3,500 g cal/dry weight). Ophiuroids generally have lowest food values (2,100 g cal/g dry weight) of the four major prey taxa consumed (Brawn et al. 1968; Cummins and Wuycheck 1971). Thus, an optimal diet based only on maximum caloric value per gram of food ingested would consist principally of crustaceans, followed by molluscs and polychaetes, and lastly of ophiuroids. However, observed diets of all sizes of Dover sole consisted primarily of ophiuroids and polychaetes, with relatively few molluscs and crustaceans. Thus, food value alone does not explain the diet of Dover sole.

The second factor determining profitability of prey, the relative expense of acquiring and digesting different prey, may play a more important role than food value in structuring the diet of Dover sole. Although no quantitative observations of feeding behavior in terms of search and handling costs have been made, some inferences can be made based on knowledge of environmental conditions and morphological features. Crustaceans were not major components of the diet, perhaps because 1) crustaceans such as amphipods may be difficult to detect in dim or turbid bottom water, 2) energy expended in pursuit of agile swimming prey may be greater than that derived from their digestion, or 3) jaw morphology may make capture of swimming crustacea difficult (Yazdani 1969, based on *Microstomus kitt*).

Molluscs may also require expenses in acquisition or digestion beyond their energetic benefits. They may be more difficult to detect and less efficiently digested than polychaetes and ophiuroids. Because the shell is not digested, digestion of molluscs such as pelecypods must take place slowly through the apertures of the shell. Calcium from the shell may also raise pH in the gut, thereby reducing efficiency of gastric enzymes. The optimal pH level for enzymes found in the stomachs of

plaice, *Pleuronectes platessa*, lies between 1.5 and 2.5; and stomach enzyme activity in plaice may cease at pH levels above 5.5 (Bayliss 1935). However, optimal pH levels in Dover sole stomachs and effects of food on local pH levels are unknown.

Relatively indigestible, low caloric ophiuroid arms were surprisingly abundant in the stomachs of Dover sole. Rae (1956) reported frequent occurrences (up to 30% of stomachs sampled) of ophiuroids in the guts of lemon sole, *Microstomus kitt*. Ophiuroids may be easy to capture and readily available. Alternatively, they could provide some required nutrient unavailable in other food sources. Finally, different rates of stomach evacuation and digestion could affect our results. The importance of ophiuroids may be easily overestimated because ophiuroids may remain in the stomach longer than the soft-bodied polychaetes, small molluscs, or crustaceans. Their arms were frequently tangled in a bulky, inflexible mass which may move slowly through the digestive tract. If a stomach contained only one or two food items, ophiuroid arms were usually present. Less digestible food items in the diet of fishes often have slower gastric evacuation rates (Fänge and Grove 1979). This would result in a longer "residence time" for ophiuroids than other prey taxa and suggests that the diet of Dover sole is principally composed of polychaetes. De Groot (1971) categorized *M. pacificus* as a polychaete-mollusc-(echinoderm) feeder, characterized by a small esophagus and stomach and complicated intestinal loop, an adaptation characteristic of flatfishes which feed on polychaetes which are often contaminated with indigestible items, e.g., tubes.

On first inspection, it appears that Dover sole do not feed more selectively on energetically more profitable prey when these prey types are more common. For example, the value of E of polychaetes at SG29 was lower than at SG10 (0.13 vs. 0.33, Table 5) while the abundance of polychaetes at SG29 was higher than at SG10 (886 vs. 396/m^2; 66% vs. 27% of the total numbers of benthic animals in the box cores (Table 7)). However, the frequency of occurrence of principal prey often changed with fish size at SG29, indicating prey selection, whereas most prey species occurred at statistically equal frequencies over the entire size range of fish sampled at SG10.

These size-related changes in selectivity at the two locations may be related to availability or energetic advantage of the prey. Prey body size was significantly correlated with size of fish at which a prey increased in importance in diet at SG29 (Figure 4). Large fish were apparently more successful than small fish at capturing large prey. Small fish may be limited to smaller, slower moving or weaker prey by mouth size or body strength. These predator-prey size relationships are consistent with those observed by Schoener (1971) for *Anolis* lizards: as predator size increased, average prey size increased. Ross (1978) also reported that mean size of prey increased with fish size for the leopard sea robin *Prionotus scitulis*, >90 mm.

Depth of prey in sediment is also significantly correlated with size of fish at which a prey species begins to occur more significantly (SG29; Figure 6). Although prey depth and prey body size were not statistically correlated, the small-bodied prey found deep in the sediment were usually not the same species which increased in frequency in larger fish. Thus, large fish apparently are physically capable of extracting large-bodied, deeply buried prey from sediment while smaller fish are not. Learning as well as extraction capability may be important in successful extraction of large polychaetes.

Since the distribution of prey species was shallower at SG10 than at SG29, the physical advantage afforded large fish in the exploitation of prey buried deep in the sediments may be eliminated at SG10. When depths of species common to both stations were compared, nearly all species were found closer to the surface at SG10, although the differences are not often statistically significant because of small sample size at SG10.

Two potential instances of increased selectivity in the face of increased abundance of a profitable or preferred prey are suggested in this study. First, the abundance of polychaetes, a preferred taxon, was lower at SG10 than SG29 (Table 7). Few significant changes in the frequency of occurrence of prey occurred with fish size at SG10 where large fish may have had to consume any polychaete encountered, regardless of size and/or location, to meet their energetic requirements. In other words, the energetic advantage arising from size-selective specialization may disappear as abundance of preferred food items decreases, as found for bluegills by Werner and Hall (1974).

Second, size-related availability results in differing effective prey densities to larger vs. smaller fish at SG29. As fish size increases, a wider range of prey may become available and so prey densities are effectively higher for larger fish. Selectivity increases with fish size (Figure 5). Since body size

of prey is also correlated with fish size, it can again be concluded that selectivity increases with an increase in densities of profitable prey.

Even though large fish at SG29 strongly selected large-bodied prey, some small-bodied prey showed no statistically significant change in frequency over the entire size range of fish. These small prey may still be "profitable" to capture by large fish. Large fish at SG29 generally consumed a wider variety of prey than small fish. The number of large-sized prey species which increased in frequency with fish size was greater than the number of small-sized species which decreased with fish length. Thus, although large-size fish consumed large-sized prey more often than small fish, they also consumed a larger range of prey sizes than did small fish.

SUMMARY

1. Dover sole off the Oregon coast in midsummer of 1976 were polychaete-ophiuroid-mollusc feeders, according to analysis of stomach contents. Polychaetes and ophiuroids were more important than molluscs and crustaceans as food in terms of frequency of occurrence, weight, and numbers.

2. Dover sole were selective feeders. Polychaetes and ophiuroids were positively selected and composed higher proportions of fish diets than of box core samples from the same location. Molluscs were not generally selected. Crustaceans were selected (SG29) or nonselectively consumed (SG10).

3. Dependency of diet on fish size varied with location. Dover sole sampled in a region of high polychaete abundance (SG29) showed size-related changes in diet. Dover sole sampled in a region of relatively low polychaete abundance (SG10) showed few size-related changes in diet.

4. When size-related changes in diet were observed, prey body size was positively correlated with predator length at which the prey taxon showed a significant increase in frequency of occurrence.

5. Consumption of polychaetes by Dover sole was a function of depth of prey taxon within the sediment and size of the fish consuming the prey. The mean depth of a prey taxon within the sediment was positively correlated with the predator length at which the prey taxon showed a significant increase in frequency of occurrence (SG29). Where polychaetes were distributed closer to the surface, few size-related changes were observed.

ACKNOWLEDGMENTS

This study was funded by the NOAA Office of Sea Grant, No. 04-5-158-2. We are especially grateful to K. Jefferts, J. Dickinson, and M. Richardson for identifying polychaetes, amphipods, and cumaceans, respectively, and to H. Jones and E. Ruff for information on mollusc and ophiuroid identification. We thank A. G. Carey, Jr., who described infaunal abundances from box core samples, and A. V. Tyler, who suggested statistical approaches to this problem.

LITERATURE CITED

ARNTZ, W. E.
1978. The "upper part" of the benthic food web: the role of macrobenthos in the western Baltic. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:85-100.

BARNES, R. D.
1968. Invertebrate zoology. 2d ed. W. B. Saunders Co., Phila., 743 p.

BAYLISS, L. E.
1935. Digestion in the plaice (*Pleuronectes platessa*). J. Mar. Biol. Assoc. U.K. 20:73-91.

BERTRAND, G. A., JR.
1971. A comparative study of the infauna of the central Oregon continental shelf. Ph.D. Thesis, Oregon State Univ., Corvallis, 123 p.

BOUMA, A. H.
1969. Methods for the study of sedimentary structures. Wiley, N.Y., 458 p.

BRAWN, V. M., D. L. PEER, AND R. J. BENTLEY.
1968. Caloric content of the standing crop of benthic and epibenthic invertebrates of St. Margaret's Bay, Nova Scotia. J. Fish. Res. Board Can. 25:1803-1811.

CAREY, A. G., JR., AND H. HEYAMOTO.
1972. Techniques and equipment for sampling benthic organisms. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, p. 378-408. Univ. Wash. Press, Seattle.

CUMMINS, K. W., AND J. C. WUYCHECK.
1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Theor. Angew. Limnol. 18, 158 p.

FÄNGE, R., AND D. GROVE.
1979. Digestion. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology, Vol. VIII, p. 161-260. Acad. Press, N.Y.

DE GROOT, S. J.
1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). Neth. J. Sea Res. 5:121-196.

HAGERMAN, F. B.
1952. The biology of the Dover sole, *Microstomus pacificus* (Lockington). Calif. Dep. Fish Game, Fish Bull. 85, 48 p.

HESSLER, R. R., AND P. A. JUMARS.
1974. Abyssal community analysis from replicate box cores in the central North Pacific. Deep-Sea Res. 21:185-209.

HOWMILLER, R. P.
1972. Effects of preservatives on weights of some common macrobenthic invertebrates. Trans. Am. Fish. Soc. 101:743-746.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Conn., 302 p.

JONES, N. S.
1952. The bottom fauna and the food of flatfish off the Cumberland coast. J. Anim. Ecol. 21:182-205.

JUMARS, P. A., AND K. FAUCHALD.
1977. Between-community contrasts in successful polychaete feeding strategies. *In* B. C. Coull (editor), Ecology of marine benthos, p. 1-20. Univ. S.C. Press, Columbia.

KREBS, J. R.
1978. Optimal foraging: decision rules for predators. *In* J. R. Krebs and N. B. Davies (editors), Behavioural ecology an evolutionary approach, p. 23-63. Blackwell Sci. Publ., Lond.

LEVINGS, C. D.
1974. Seasonal changes in feeding and particle selection by winter flounder (*Pseudopleuronectes americanus*). Trans. Am. Fish. Soc. 103:828-832.

MALONEY, N. J.
1965. Geology of the continental terrace off the central coast of Oregon. Ph.D. Thesis, Oregon State Univ., Corvallis, 233 p.

MOORE, J. W., AND I. A. MOORE.
1976. The basis of food selection in flounders, *Platichthys flesus* (L.), in the Severn Estuary. J. Fish Biol. 9:139-156.

PEARCY, W. G.
1978. Distribution and abundance of small flatfishes and other demersal fishes in a region of diverse sediments and bathymetry off Oregon. Fish. Bull., U.S. 76:629-640.

PEARCY, W. G., AND D. HANCOCK.
1978. Feeding habits of Dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; slender sole, *Lyopsetta exilis*; and Pacific sanddab, *Citharichthys sordidus*, in a region of diverse sediments and bathymetry off Oregon. Fish. Bull., U.S. 76:641-651.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV.
1977. Optimal foraging: A selective review of theory and tests. Q. Rev. Biol. 52:137-154.

RAE, B. B.
1956. The food and feeding habits of the Lemon sole. Mar. Res. Scott. Home Dep. 1956(3), 32 p.

ROSS, S. T.
1978. Trophic ontogeny of the leopard searobin, *Prionotus scitulus* (Pisces: Triglidae). Fish. Bull., U.S. 76:225-234.

SCHOENER, T. W.
1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369-404.

SMITH, R. I., AND J. T. CARLTON (editors).
1975. Light's manual: Intertidal invertebrates of the Central California coast. 3d ed. Univ. Calif. Press, Berkeley, 716 p.

SOKAL, R. R., AND J. J. ROHLF.
1969. Biometry. W. H. Freeman, San Franc., 776 p.

STEVEN, G. A.
1930. Bottom fauna and the food of fishes. J. Mar. Biol. Assoc. U.K. 16:677-700.

THORSON, G.
1957. Bottom communities (sublittoral or shallow shelf). *In* J. W. Hedgpeth (editor), Treatise on marine ecology and paleoecology, p. 461-534. Geol. Soc. Am. Mem. 67, vol. 1.

TYLER, A. V.
1973. Caloric values of some North Atlantic invertebrates. Mar. Biol. (Berl.) 19:258-261.

WERNER, E. E., AND D. J. HALL.
1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042-1052.

YAZDANI, G. M.
1969. Adaptation in the jaws of flatfish (Pleuronectiformes). J. Zool. (Lond.) 159:181-222.

CEPHALOPODS IN THE DIET OF THE SWORDFISH, *XIPHIAS GLADIUS*, FROM THE FLORIDA STRAITS

RONALD B. TOLL AND STEVEN C. HESS[1]

ABSTRACT

An analysis was conducted on the cephalopod remains from the stomachs of 65 swordfish, *Xiphias gladius*, from the Florida Straits. Results indicated that cephalopods contribute a large proportion of the total ration of food items, accounting for over 90% of total weight of contents in 69% of the stomachs. Of these, ommastrephid squid of the genus *Illex* represented the single most important prey items. In total, 15 species of cephalopods were encountered, consisting of 13 teuthoids and 2 octopods. This previously unrecognized diversity confirmed the earlier postulated opportunistic feeding strategy of *X. gladius*. Cephalopod, fish, and crustacean remains are reported in terms of frequency of occurrence and biomass. Analysis of the vertical distribution of cephalopod prey indicated that swordfish feeding is most concentrated in epipelagic and upper mesopelagic waters. Comparisons with feeding studies on billfishes from the western North Atlantic indicated that istiophorids may rely more heavily on finfish prey than squid in contrast with the present findings for *X. gladius*. Also, octopods may contribute a greater proportion of the cephalopod component of total ration in the istiophorids than in *X. gladius*.

Analysis of stomach contents of many marine teleosts, mammals, and birds (Bouxin and Le Gendre 1936; Clarke 1966; Rancurel 1970, 1976; Dragovich and Potthoff 1972; Imber 1973, 1975; Perrin et al. 1973; Clarke and MacLeod 1970, 1976; Mercer 1974) coupled with estimates of cephalopod biomass (Voss 1973) suggest a key role of cephalopods in oceanic food webs. Nevertheless, few thorough studies have been conducted that have analyzed cephalopod remains, both qualitatively and quantitatively (see Voss 1953; Rees and Maul 1956; Jolley 1977; Matthews et al. 1977; Morejohn et al. 1978). Oceanic vertebrates are often more efficient collectors of cephalopods than available oceanographic gear (Clarke 1966). Therefore, information from stomach content analyses can supplement and refine existing knowledge of the biology of both prey and predator.

Cephalopods represent a major element in the diet of the swordfish, *Xiphias gladius* Linnaeus (Maksimov 1969). Yet, investigations of swordfish diet, commencing with Fleming (1828), yield little data concerning the trophic relationship between this predator and cephalopod mollusks. Acquisition of 65 swordfish stomachs allowed investigation of feeding ecology with emphasis on aspects of the biology and systematics of cephalopod prey.

[1]Division of Biology and Living Resources, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149.

Manuscript accepted July 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

HISTORICAL RESUMÉ

The feeding ecology of *X. gladius* is poorly understood, not only because of a general paucity of studies concerning xiphiid predation, but perhaps more importantly, from a lack of studies by invertebrate specialists dealing with invertebrates consumed by swordfish (e.g., mollusks, crustaceans). In contrast, stomach content analyses made by ichthyologists have provided reasonably good specific-level diagnoses of fish remains. A brief summary of studies that contain information on cephalopod remains from *X. gladius* stomachs is provided here.

Goode (1883) cited Fleming's (1828) report of the remains of *Sepiae* from a swordfish stomach. Goode also noted the occurrence of squid mandibles and speculated they were from the loliginid squid, *Loligo Pealii* (= *L. pealei*). In addition, Goode observed that stomach contents of swordfish from the western Atlantic were "...for the most part of the common schooling species of fishes." Rich (1947) noted a set of large beaks ("perhaps *Architeuthis*") from a *Xiphias* harpooned on the northern Georges Banks. Bigelow and Schroeder (1953) noted a specimen of *Ilex* (= *Illex*) from the stomach of a swordfish harpooned off Halifax, Nova Scotia, and commented that squid may, at times, form the chief component of the swordfish diet. Yabe et al. (1959) reported squid (mantle length 20-40 mm) and

squid fragments (mantles and beaks) from several swordfish stomachs. They did not assign these cephalopod remains to more specific taxa. Several specimens contained "octopus jaws." Their study demonstrated ontogenetic changes in prey selection, with adult Pacific swordfish feeding principally on squid. Tibbo et al. (1961) examined stomachs of 39 swordfish from Nantucket Shoals and Sable Island Bank, finding fish and the squid *Illex illecebrosus*. In 14 of those swordfish (Sable Island Bank specimens), 22 squid were included among 564 food items.

De Sylva (1962) analyzed stomachs of seven female swordfish caught in April to May off northern Chile. Of the five specimens containing food remains, 24 squid *Dosidicus gigas* were found. These findings led de Sylva to believe that most swordfish feeding takes place near the surface. Cavaliere (1963) reported swordfish diets from the Straits of Messina and adjacent waters during spring and summer. Cephalopods were found in 80% of the stomachs with *I. coindetii*, *L. todarus* (= *Todarodes sagittatus* ?), and *Todarodes sagittatus* being most common. Guitart-Manday (1964), reporting on an unspecified number of swordfish taken during February and March near Cuba, found teuthoids, including *Thysanoteuthis rhombus* and a single octopod, constituting approximately 30% of the diet by number of items. Scott and Tibbo (1968), utilizing volumetric analysis, examined stomach contents of 514 swordfish from the western North Atlantic between Virginia and Sable Island Banks. They reported that, from March to October, swordfish feed on *I. illecebrosus*, as well as on a variety of fishes. Scott and Tibbo also noted the occurrence of the squid *Ommastrephes*. Interestingly, they reported the infrequent occurrence of the octopod, *Bathypolypus arcticus*, a benthic inhabitant of the continental shelf.

Maksimov (1969) examined stomach contents from 502 swordfish from the tropical Atlantic. Frequency of occurrence and average size of food items were reported. Cephalopods were a major component of the diet in all areas sampled. The following organisms were represented: *Loligo* sp., *Ommastrephes* sp. (3 undetermined spp.), and an undetermined species of sepioid. Ovchinnikov (1970) noted cephalopod and fish remains by percentage from swordfish taken near Cuba. They are identical to those reported by Guitart-Manday (1964) and probably are an uncited repetition of the same data. Beckett (1974) reported swordfish diets from the northwest Atlantic. He indicated that swordfish over deep water usually feed on vertically migrating species including squids, however, no further taxonomic breakdown was given.

MATERIALS AND METHODS

Food remains from the stomachs of 65 specimens of *X. gladius* from the Straits of Florida were examined. Samples were obtained from three sources: sportfishing tournaments in Miami and Ft. Lauderdale, Fla. (38 specimens), commercial longliners (23 specimens), and other sources (4 specimens). Collection data are given in Appendix Table 1.

Tournament swordfish specimens were measured and weighed at dockside. Weights of longline specimens were estimated using fork length-weight relationships for both males and females (Southeast Fisheries Center[2]). Stomachs were removed and the contents fixed in 10% Formalin.[3] Following fixation, samples were transferred to 70% ethyl alcohol for storage.

Analysis of individual stomachs was conducted as follows. Contents were separated into squid, fish, and other invertebrate components. Total weights were taken for each group. Remains of intact squid were further analyzed for individual weight, dorsal mantle length, sex, state of maturity, and general condition. Based on available morphological features, squid were assigned to the lowest possible taxa. Because of the poor condition of many squid, numerous systematic characters often were destroyed or unrecognizable. Most species-specific diagnoses of teuthoid cephalopods are based on external, soft-tissue characters. It is just those features that are subject to the intial effects of digestion. As a result, identifications were based on a composite of less frequently utilized morphological features that are more resistant to digestive enzymes. These included gladius and spermatophore morphology, internal anatomy, dermal cartilage, mantle musculature, photophore number and distribution, salient beak characters, and radulae. The potential utility of such characters to predator-

[2]Southeast Fisheries Center. 1981. Report of the ICCAT Inter-sessional Workshop on Billfish. Natl. Mar. Fish. Serv., Southeast Fish. Cent., Miami, Fla., Doc. 8, 16 p. Unpubl. manuscr.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

prey studies by nonteuthologists has prompted the writers to begin work on a guide to identification of cephalopod remains from predatory species.

Buccal masses were dissected from identified squid remains and retained for future examination of mandibles. Estimates of the number of cephalopods were based solely on soft-tissue remains. Unassociated hard structures such as free mandibles, lenses, and gladii often were encountered in large numbers suggesting extended residence within the stomach. Therefore, inventories of those remains were not utilized in determining total numbers of cephalopod prey.

An attempt was made to assess the vertical migratory behavior of swordfish based on known bathymetric distribution of their squid prey. Other aspects of swordfish feeding ecology were examined using fishing depth and hookup time, as well as sex and size of swordfish specimens.

RESULTS

Tables 1 and 2 present frequencies and biomasses of prey in stomachs of 65 swordfish. Cephalopods were the most important component, both in numbers and weight. Fish remains were of secondary importance, followed by crustaceans (shrimp). Figures 1-3 depict frequency of occurrence of each group. Cephalopods composed over 90% of the contents by weight in 68% of the stomachs examined. Only 9% of the stomachs contained <50% cephalopod remains. Fish remains accounted for >50% of contents in only 11% of the stomachs. Fish remains were ≤10% of total remains in 69% of all stomachs. Shrimp remains were found in only 9% of the stomachs, accounting for 8% by weight in one stomach and <3% in all other instances. Weights of stomach contents are conservative because swordfish are known to occasionally regurgitate or even evert their stomach when captured (Tibbo et al. 1961).

Cephalopod remains were found to include the following species:

Class: Cephalopoda Cuvier 1798
- Subclass: Coleoidea Bather 1888
  - Order: Teuthoidea Naef 1916
    - Suborder: Oegopsida Orbigny 1845
      - Family: Enoploteuthidae Pfeffer 1900
        - Subfamily: Ancistrocheirinae Pfeffer 1912
          - Genus: *Ancistrocheirus* Gray 1849
            - Species: *A. lesueuri* (Orbigny 1839)
      - Family: Onychoteuthidae Gray 1849
        - Genus: *Onychoteuthis* Lichtenstein 1818
          - Species: *O. banksii* (Leach 1817)
      - Family: Lepidoteuthidae Naef 1912
        - Genus: *Tetronychoteuthis* Pfeffer 1900
          - Species: *T. massyae* Pfeffer 1912
      - Family: Architeuthidae Pfeffer 1900
        - Genus: *Architeuthis* Steenstrup 1857
          - Species: *Architeuthis* sp.
      - Family: Histioteuthidae Verrill 1881
        - Genus: *Histioteuthis* Orbigny 1841
          - Species: *H. dofleini* (Pfeffer 1912)
          - *Histioteuthis* sp.
      - Family: Ctenopterygidae Grimpe 1922
        - Genus: *Ctenopteryx* Appellöf 1899
          - Species: *C. sicula* (Verany 1851)
      - Family: Ommastrephidae Steenstrup 1857
        - Subfamily: Ommastrephinae Steenstrup 1857
          - Genus: *Ommastrephes* Orbigny 1835
            - Species: *O. pteropus* Steenstrup 1855
          - Genus: *Ornithoteuthis* Okada 1927
            - Species: *O. antillarum* (Adam 1957)
        - Subfamily: Illicinae Posselt 1890
          - Genus: *Illex* Steenstrup 1880
            - Species: *I. coindetii* ? (Verany 1837)
            - *I. oxygonius* Roper, Lu, and Mangold 1969
            - *I. illecebrosus* ? Lesueur 1821
      - Family: Thysanoteuthidae Keferstein 1866
        - Genus: *Thysanoteuthis* Troschel 1857
          - Species: *T. rhombus* Troschel 1857
      - Family: Cranchiidae Prosch 1849
        - Subfamily: Cranchiinae Prosch 1849
          - Genus: *Cranchia* Leach 1817
            - Species: *C. scabra* Leach 1817
- Order: Octopoda Leach 1818
  - Suborder: Incirrata Grimpe 1916
    - Family: Bolitaenidae Chun 1911
      - Genus: *Japetella* Hoyle 1885
        - Species: *J. diaphana* Hoyle 1885

Family: Argonautidae Naef 1912
Genus: *Argonauta* Linnaeus 1758
Species: *Argonauta* sp.

Octopod remains were limited to a single occurrence of each of two species, both taken from the same stomach. Remaining cephalopods consisted of squid of the suborder Oegopsida. Of these, the genus *Illex* was predominant (Figure 4). *Histioteuthis* was second most common based on number of individuals, followed by equal numbers of *Ommastrephes pteropus* and *Onychoteuthis banksii*. Following these, in decreasing frequency of occurrence were *Thysanoteuthis rhombus* and *Cranchia scabra*. There were single records of *Ornithoteuthis antillarum*, *Tetronychoteuthis massyae*, *Ancistrocheirus lesueuri*, *Ctenopteryx sicula*, and *Architeuthis* sp. Because *Ommastrephes pteropus* and *Thysanoteuthis rhombus* reach large sizes, their contribution to prey biomass was more important than reflected by number of individuals.

Comparison of prey composition and quantity relative to swordfish sex, size, capture method, hookup time, and time of year did not reveal any correlations.

TABLE 1.—Diversity and abundance (number of individuals) of cephalopod remains in the stomach contents of *Xiphias gladius*.

	Order Teuthoidea												Order Octopoda		Other cephalopod remains				
Fish no.[1]	*Illex* spp.[2]	*Ommastrephes pteropus*	*Ornithoteuthis antillarum*	*Ancistrocheirus lesueuri*	*Onychoteuthis banksii*	*Tetronychoteuthis massyae*	*Architeuthis* sp.	*Histioteuthis dofleini*	*Histioteuthis* sp.[3]	*Ctenopteryx sicula*	*Thysanoteuthis rhombus*	*Cranchia scabra*	*Japetella diaphana*	*Argonauta* sp.	Soft-tissue fragments	Buccal masses[4]	Mandibles[4]	Gladii (Ommastrephidae)[4]	Lenses[4]	Total
1	15				1										1					17
2	7														2+	1	42	18+	32	9+
3	10																1			10
4	2														5+		32	19+		7+
5	3	1													2+		40			6+
6	13	1															14			14
7	1																			1
8	27	1			1		1								5+	5	23	2	4	35+
9	28														2+					30+
10	1														2+					3+
11	1																23			1
12	2															6	19			2
13	1														1+		8			2+
14															2+	2	2			2+
15	1	1														4	4		3	2
16	2														1+	1	6			3+
17															1+	1	66	14+		1+
18		1													4+	4				5+
19	15										1				2+	2				18+
20	8														5+		46	25	29	13+
21									1							5	4	5	6	1
22															13+	3		10	24	13+
23	13														1				17	14
24	9																			9
25	14														6+		11		11	20+
26	12																			12
27	2							1							16+	6		16	15	19+
28	5				3											5	63	53	78	8
29																			51	0
30															13+	4	35	34	12	13+
31	10														19+		16	18	31	29+
32	5														4+	7	8	7+		9+
33															1					1
34	2														7+	2	25	6+		9+
35	13	1													9+	8	96	25+		23+
36					2										2+			13	24	4+
37															1+	1	12	6	3	1+
38	17																			17
39	7														3+				4	10+
40	10														4+		42	15	41	14+
41															1+		38	22	12	1+
42															9+	8	23	18		9+
43	1														4+	3	2	10	13	5+

TABLE 1.—*Continued.*

	Order Teuthoidea												Order Octopoda		Other cephalopod remains					
Fish no.[1]	*Illex* spp.[2]	*Ommastrephes pteropus*	*Ornithoteuthis antillarum*	*Ancistrocheirus lesueuri*	*Onychoteuthis banksii*	*Tetronychoteuthis massyae*	*Architeuthis* sp.	*Histioteuthis dofleini*	*Histioteuthis* sp.[3]	*Ctenopteryx sicula*	*Thysanoteuthis rhombus*	*Cranchia scabra*	*Japetella diaphana*	*Argonauta* sp.	Soft-tissue fragments	Buccal masses[4]	Mandibles[4]	Gladii (Ommastrephidae)[4]	Lenses[4]	Total
44	1										1				3+	1	4	4		5+
45	1										1				4+	3	18	13	16	5+
46															10+	7	16	22	19	10+
47															8+	2		2	5	8+
48	7														4+	10		4	12	11+
49	2														6+	1	20	10+	44	8+
50	6														2+	3	4	2	1	8+
51															9+	2	12	18	13	9+
52	5														1					7
53	1																			1
54	4														3+					7+
55	1											1								2
56			1																	1
57						1				1		1								3
58								1					1	1						3
59		1																		1
60	4								4						1+		8			9+
61								1												1
62	4														1+	2	22	12		5+
63	8																56	28		8
64	7														2+	2	6	8	13	9+
65				1					1						1+		2	2		3+

[1]See Appendix Table 1.
[2]Includes *I. coindetii*, *I. illecebrosus*, and *I. oxygonius* (see Discussion).
[3]May include more than one species.
[4]Not included in total cephalopods (see Materials and Methods).

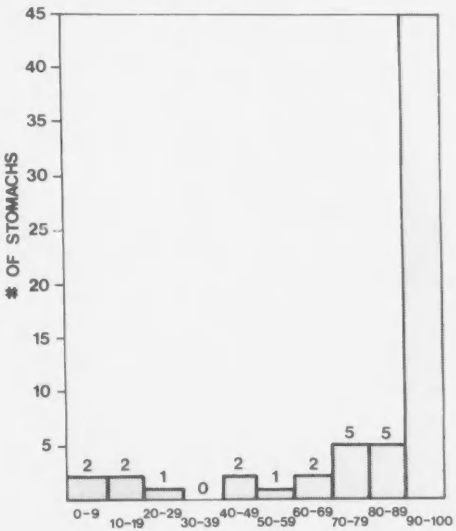

FIGURE 1.—Cephalopod remains as percent of total stomach contents by weight.

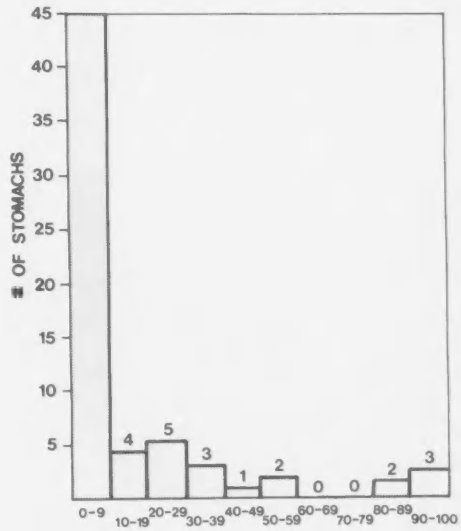

FIGURE 2.—Fish remains as percent of total stomach contents by weight.

TABLE 2.—Weights (grams) of cephalopod, fish, and other invertebrate remains in the stomach contents of *Xiphias gladius*.

	Order Teuthoidea												Order Octopoda		Total			Percent of total			
Fish no.[1]	*Illex* spp.[2]	*Ommastrephes pteropus*	*Ornithoteuthis antillarum*	*Ancistrocheirus lesueuri*	*Onychoteuthis banksii*	*Tetronychoteuthis massyae*	*Architeuthis* sp.	*Histioteuthis dofleini*	*Histioteuthis* sp.[3]	*Ctenopteryx sicula*	*Thysanoteuthis rhombus*	*Cranchia scabra*	*Japetella diaphana*	*Argonauta* sp.	Cephalopods	Fish	Other invertebrates (shrimp)	Cephalopods[4]	Fish	Other invertebrates (shrimp)	Total of all components
1	1,033				36										1,088	1	0	>99	<1	0	1,089
2	421														477	24	1	95	4	<1	502
3	1,062														1,062	0	0	100	0	0	1,062
4	88														213	0	0	100	0	0	213
5	178	334													614	0	0	100	0	0	614
6	1,316	319													1,635	0	0	100	0	0	1,635
7	73														73	10	0	88	12	0	83
8	3,023	155			70		107								3,730	72	0	98	2	0	3,802
9	2,726														2,812	0	0	100	0	0	2,812
10	61														145	0	4	97	0	3	149
11	177														177	1	0	>99	<1	0	178
12	155														155	0	0	100	0	0	155
13	80														141	0	0	100	0	0	141
14															141	20	0	88	12	0	161
15	49	475													524	0	0	100	0	0	524
16	263														263	0	23	92	0	8	286
17															4	88	1	4	>95	<1	93
18		661													859	77	0	92	8	0	936
19	2,471											75			2,642	214	0	93	7	0	2,856
20	811														994	75	0	93	7	0	1,069
21										2					15	61	0	20	80	0	76
22															795	0	11	98	0	2	806
23	1,059														1,091	0	0	100	0	0	1,091
24	1,131														1,131	0	0	100	0	0	1,131
25	1,517														1,993	93	0	96	4	0	2,086
26	1,553														1,553	0	0	100	0	0	1,553
27	178							45							223	0	0	100	0	0	223
28	395				2										397	0	0	100	0	0	397
29															—	0	0	100	0	0	—
30															505	0	0	100	0	0	505
31	689														1,328	162	0	89	11	0	1,490
32	387														531	39	0	93	7	0	570
33															36	319	0	10	90	0	355
34	80														362	445	0	45	55	0	807
35	1,090	375													1,871	11	0	99	1	0	1,882
36					2										140	725	0	16	84	0	865
37															24	10	0	71	29	0	34
38	1,273														1,273	0	0	100	0	0	1,273
39	572														715	26	0	96	4	0	741
40	569														644	21	0	97	3	0	665
41															78	0	0	100	0	0	78
42															419	388	0	52	48	0	807
43	114														163	0	0	100	0	0	163
44	108											487			675	287	0	70	30	0	962
45	98											6			161	44	0	79	21	0	205
46															408	116	0	78	22	0	524
47															426	76	0	85	15	0	502
48	644														678	0	0	100	0	0	678
49	226														574	21	0	96	4	0	595
50	627														650	0	0	100	0	0	650
51															389	242	0	62	38	0	631
52	768														838	0	0	100	0	0	838
53	151														151	73	0	77	23	0	224
54	684														789	200	0	80	20	0	989
55	93												7		100	0	0	100	0	0	100
56			12												12	0	0	100	0	0	12
57						15					85		5		105	0	0	100	0	0	105
58								1						2 1	4	992	2	<1	>99	<1	998
59		146													146	73	0	67	33	0	219
60	379								235						679	0	0	100	0	0	679
61								164							164	0	0	100	0	0	164
62	446														468	34	0	93	7	0	502
63	617														628	0	0	100	0	0	628
64	600														713	0	0	100	0	0	713
65				26					209						391	420	0	48	52	0	811

[1] See Appendix Table 1.
[2] Includes *I. coindetii*, *I. illecebrosus*, and *I. oxygonius* (see Discussion).
[3] May include more than one species.
[4] Includes weights of fragments.

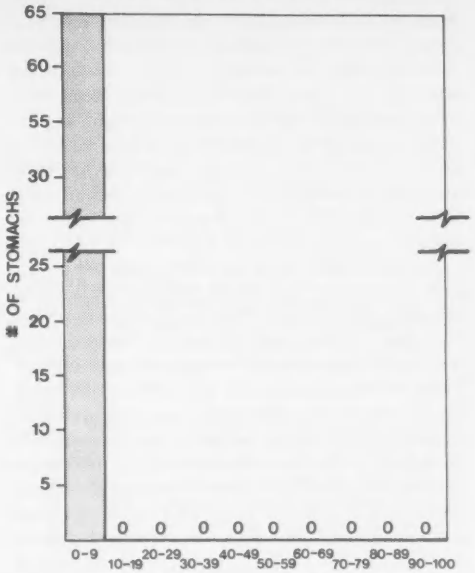

FIGURE 3.—Shrimp remains as percent of total stomach contents by weight.

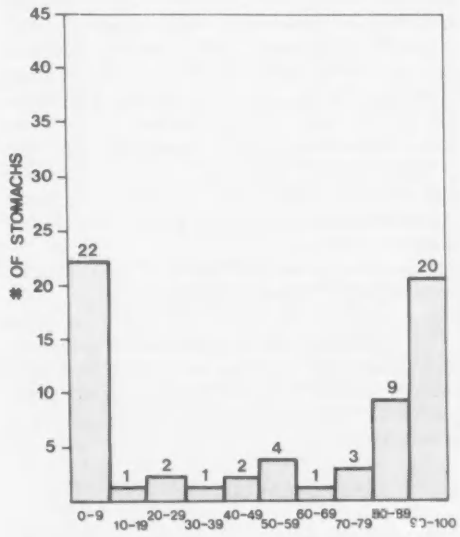

FIGURE 4.—*Illex* spp. remains as percent of total stomach contents by weight.

DISCUSSION

Swordfish in the Straits of Florida demonstrate a clear predilection for cephalopods as prey, specifically squids. Furthermore, the genus *Illex* constitutes the single most important component in the diet. At present, there are three nominal species of *Illex* known from the western North Atlantic: *I. illecebrosus*, *I. coindetii*, and *I. oxygonius*. A recent revision (Roper et al. 1969) attempted to stabilize the systematic positions of these taxa. However, the same authors reemphasized systematic and distributional complexities of this polytypic genus, especially in the tropical western Atlantic which includes the present study area. Numerous specimens examined in this work had the specific characters assigned to their nominal species, however, systematic problems appear to be most acute in the *I. illecebrosus-I. coindetii* complex. Because of the tenuous systematic and distributional aspects, as well as the poor condition of much of the material, the writers thought it best to deal with the group at the generic level rather than possibly adding to the underlying systematic and zoogeographic confusion.

Many teuthoids aggregate for feeding or reproduction (see Clarke 1966). The cephalopod prey in this study included such aggregating squid as *Illex* spp., *Ommastrephes pteropus*, *Thysanoteuthis rhombus*, *Onychoteuthis banksii*, and *Histioteuthis* sp. Additionally, *Ornithoteuthis antillarum* and *Tetronychoteuthis massyae* probably behave similarly. Heavy swordfish predation upon aggregating or schooling cephalopods is similar to reported predation on schooling fishes (Goode 1883; Tibbo et al. 1961). Tibbo et al. (1961) and Scott and Tibbo (1968) noted the use of the bill by swordfish to wound or kill prey. They suggested that swordfish slash laterally with their bills, while ascending or descending through a school of prey. The present material contained numerous decapitated squid and more frequently, oblique slash marks on mantles thus supporting the postulated foraging behavior. Furthermore, this concurs with the known horizontal orientation of the pelagic squids listed above. Ommastrephids and *Thysanoteuthis* have muscular mantles and are powerful swimmers. Swimming ability of swordfish does not appear to be a limiting factor in the selection of cephalopod prey, as indicated by the predominance of these organisms in the diet of *X. gladius*.

In the tropics, swordfish undergo daily vertical migrations, rising to feed near the surface at night and returning to deeper waters by day (Beardsley 1978). The full extent of these vertical migrations is poorly known. Cephalopods also exhibit vertical distributions and diel migrations of considerable range (Voss 1967; Clarke and Lu 1974, 1975; Lu and Clark 1975a, b; Roper and Young 1975; Herring 1977). While these works provide some data on bathymetric distribution suggesting general patterns of vertical migration, the actual distributions of most cephalopod species remain poorly known. At the familial level, all but three of the cephalopods encountered in this work may occur from the surface to depths between 500 and 1,000 m. Histioteuthids are found from near the surface to about 2,500 m. Cranchiids range, in general, from the surface to about 3,000 m, but the only species found in swordfish stomachs, *Cranchia scabra*, is confined to the upper several hundred meters of the water column (N. Voss[4]). Thore (1949) stated that adults of *Japetella diaphana* are found in 330-3,000 m of water, while younger animals are concentrated at depths of 100-330 m. Bathymetric ranges of all cephalopod species considered here encompass the upper 500 m of water. While it remains possible that swordfish forage at greater depths, it appears that most feeding is concentrated in epipelagic and upper mesopelagic waters.

This analysis of the cephalopod component of the swordfish diet supports earlier observations (Scott and Tibbo 1968), suggesting the opportunistic nature of *X. gladius* predation. Based on the data presented here, prey composition is independent of season, fish size, or sex. Rather, stomach contents appear to reflect the diversity and relative abundance of potential prey.

Voss (1953) examined stomach contents of 241 sailfish, *Istiophorus americanus* (= *I. platypterus*), from Florida waters. Of 461 identified prey, 83% were fish, including members of at least 20 families. A total of 78 cephalopods, including 27 octopods, were found. Voss identified the octopod specimens as *Argonauta argo*, *Argonauta* sp., and *Grimpoteuthis*?. Of the 49 teuthoids recovered, all were considered *Sthenoteuthis bartrami* (= *Ommastrephes bartrami*), but probably were *O. pteropus*. Maksimov (1971) examined stomachs of sailfish from the tropical Atlantic. Teuthoids and octopods predominated as food. Over 61% of sailfish stomachs from Brazil contained squid and 50% contained octopods. Sailfish taken off Barbados contained squid, but no octopods. Jolley (1977) examined 778 sailfish from off southeast Florida and found scombrid fish to be the most important prey followed by cephalopods. Jolley found 27% of all stomachs examined to be empty.

Krumholz and de Sylva (1958) reported on the stomach contents of white marlin, *Tetrapterus albidus*, taken near Bimini, Bahamas. Nine stomachs contained cephalopods, arthropods, and fish. Squid and octopods were the most abundant items, accounting for 41% and 18%, respectively, by frequency of occurrence. An additional 41 stomachs were empty. De Sylva and Davis (1963) examined stomachs of 55 white marlin from the Middle Atlantic Bight. Round herring, *Etrumeus teres*, and *Loligo pealei* were the chief components of the diet. Ovchinnikov (1970) investigated diets of white marlin in the tropical Atlantic, noting *Loligo pealei* as the most important prey.

Krumholz and de Sylva (1958) also reported on 14 blue marlin stomachs of which 10 contained food. Fish were more important than cephalopods by frequency of occurrence. Cephalopod remains consisted of the pelagic octopods *Argonauta argo* and *Ocythoe tuberculata*, which together constituted 17% of the total number of prey. Voss and Erdman (1959) reported finding a large specimen of the squid *Thysanoteuthis rhombus* in the stomach of a blue marlin caught off San Juan, Puerto Rico. Ovchinnikov (1970) investigated stomachs of blue marlin. These fish contained teuthoids and less frequently sepioids. Fish were more important than cephalopods in the diet of blue marlin.

Two observations are apparent from comparisons of diets of istiophorids and swordfish. First, fish appear to be more important in diets of istiophorids, with cephalopods of secondary importance. The opposite is true for swordfish. Second, octopods may be a more important component of the cephalopod prey of istiophorids than of swordfish.

ACKNOWLEDGMENTS

The authors wish to thank Steven Berkeley, Lise Dowd, and Mark Poli for assistance in the collection of specimens. Berkeley also provided data

[4]N. Voss, Division of Biology and Living Resources, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, FL 33149, pers. commun. July 1980.

on most swordfish specimens. Mitchell Roffer aided in the acquisition of pertinent literature. Lastly, thanks go to Gilbert L. Voss and Edward D. Houde for reviewing the manuscript.

This is a scientific contribution of the Rosenstiel School of Marine and Atmospheric Science of the University of Miami.

LITERATURE CITED

BEARDSLEY, G. L. (editor).
1978. Report of the swordfish workshop held at the Miami Laboratory, Southeast Fisheries Center, Miami, Fla. June 7-9, 1977. Coll. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas, Madrid, Vol. VII (SCRS-1977), No. 1, p. 149-158.

BECKETT, J. S.
1974. Biology of the swordfish, *Xiphias gladius* L., in the northwest Atlantic Ocean. *In* R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972. Part 2. Review and contributed papers, p. 103-106. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BOUXIN, J., AND R. LEGENDRE.
1936. La faune pélagique de l'Atlantique au large du Golfe de Gascogne, récueille dans des estomacs de germons. Ann. Inst. Oceanogr. (New Ser.) 16(1):1-99.

CAVALIERE, A.
1963. Studi sulla biologia e pesca di *Xiphias gladius* L. Nota II. Boll. Pesca Pisc. Idrobiol. 18:143-170. (Engl. transl. Fish. Res. Board Can. Transl. Ser. 2298.)

CLARKE, M. R.
1966. A review of the systematics and ecology of oceanic squids. Adv. Mar. Biol. 4:91-300.

CLARKE, M. R., AND C. C. LU.
1974. Vertical distribution of cephalopods at 30°N 23°W in the North Atlantic. J. Mar. Biol. Assoc. U.K. 54:969-984.
1975. Vertical distribution of cephalopods at 18°N 25°W in the North Atlantic. J. Mar. Biol. Assoc. U.K. 55:165-182.

CLARKE, M. R., AND N. MACLEOD.
1974. Cephalopod remains from a sperm whale caught off Vigo, Spain. J. Mar. Biol. Assoc. U.K. 54:959-968.
1976. Cephalopod remains from sperm whales caught off Iceland. J. Mar. Biol. Assoc. U.K. 56:733-749.

DE SYLVA, D. P.
1962. Red-water blooms off northern Chile, April-May 1956, with reference to the ecology of the swordfish and the striped marlin. Pac. Sci. 16:271-279.

DE SYLVA, D. P., AND W. P. DAVIS.
1963. White marlin, *Tetrapturus albidus*, in the middle Atlantic bight, with observations on the hydrography of the fishing grounds. Copeia 1963:81-99.

DRAGOVICH, A., AND T. POTTHOFF.
1972. Comparative study of food of skipjack and yellowfin tunas off the coast of West Africa. Fish. Bull., U.S. 70:1087-1110.

FLEMING, J.
1828. *A history of British animals...visitants*. Edinb. and Lond.

GOODE, G. B.
1883. Materials for a history of the sword-fish. Rep. Comm. 1880. U.S. Comm. Fish Fish. 8:289-394.

GUITART-MANDAY, D.
1964. Biología pesquera del Emperador o Pez de Espada, *Xiphias gladius* Linnaeus (Teleostomi: Xiphiidae) en las aguas de Cuba. [Engl. synop.] Poeyana Ser. B, 1, 37 p.

HERRING, P. J.
1977. Luminescence in cephalopods and fish. *In* M. Nixon and J. B. Messenger (editors), The biology of cephalopods, p. 127-159. Proc. Symp. Zool. Soc. Lond. 38.

IMBER, M. J.
1973. The food of grey-faced petrels (*Pterodroma macroptera gouldi* (Hutton)), with special reference to diurnal vertical migration of their prey. J. Anim. Ecol. 42:645-662.
1975. Lycoteuthid squids as prey of petrels in New Zealand seas. N.Z. J. Mar. Freshwater Res. 9:483-492.

JOLLEY, J. W., JR.
1977. The biology and fishery of Atlantic sailfish *Istiophorus platypterus*, from southeast Florida. Fla. Mar. Res. Publ. 28, 31 p.

KRUMHOLZ, L. A., AND D. P. DE SYLVA.
1958. Some foods of marlins near Bimini, Bahamas. Bull. Am. Mus. Nat. Hist. 114:406-411.

LU, C. C., AND M. R. CLARKE.
1975a. Vertical distribution of cephalopods at 40°N, 53°N and 60°N at 20°W in the North Atlantic. J. Mar. Biol. Assoc. U.K. 55:143-163.
1975b. Vertical distribution of cephalopods at 11°N, 20°W in the North Atlantic. J. Mar. Biol. Assoc. U.K. 55:369-389.

MAKSIMOV, V. P.
1969. Pitanie bol'skegla zogo tuntsa (*Thunnus obesus* Lowe) i mechryby (*Xiphias gladius* L.) vostochnoi chasti tropichesko i Atlantikii. Atl. Nauchno.-Issled. Inst. Rybn. Khoz. Okeanogr. (Atl. NIRO) 25:87-99. (Engl. transl. Fish. Res. Board Can. Transl. Ser. 2248.)
1971. The biology of the sailfish [*Istiophorus platypterus* (Shaw et Nodder)] in the Atlantic Ocean. J. Ichthyol. 11:850-855.

MATTHEWS, F. D., D. M. DAMKAER, L. W. KNAPP, AND B. B. COLLETTE.
1977. Food of the western North Atlantic tunas (*Thunnus*) and lancetfishes (*Alepisaurus*). U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-706, 19 p.

MERCER, M. C.
1974. Modified Leslie-DeLury assessments of the northern pilot whale (*Globicephala malaena*) and annual production of the short-finned squid (*Illex illecebrosus*) based on their interaction at Newfoundland. Int. Comm. North Atl. Fish. Res. Doc. 74/49, Ser. 3256, 14 p.

MOREJOHN, G. V., J. T. HARVEY, AND L. T. KRASNOW.
1978. The importance of *Loligo opalescens* in the food web of marine vertebrates in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 169:67-98.

OVCHINNIKOV, V. V.
1970. Swordfishes and billfishes in the Atlantic Ocean: ecology and functional morphology. (Engl. transl. by H. Mills, Isr. Program Sci. Transl., 1971, 77 p., available Natl. Tech. Inf. Serv., Springfield, Va., as TT 71-50011.)

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS.
1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull., U.S. 71:1077-1092.

RANCUREL, P.
1971. Les contenus stomacaux d'*Alepisaurus ferox* dans le sud-ouest Pacific (Céphalopodes). Cah. O.R.S.T.O.M., sér. Océanogr. 8(4):3-87.
1976. Note sur les céphalopodes des contenus stomacaux de *Thunnus albacares* (Bonnaterre) dans le sud-ouest Pacifique. Cah. O.R.S.T.O.M., sér. Océanogr. 14(1): 71-80.

REES, W. J., AND G. E. MAUL.
1956. The Cephalopoda of Madeira: records and distribution. Bull. Br. Mus. (Nat. Hist.) Zool. 3:259-281.

RICH, W. H.
1947. The swordfish and the swordfishery of New England. Proc. Portland Soc. Nat. Hist. 4(2), 102 p.

ROPER, C. F. E., C. C. LU, AND K. MANGOLD.
1969. A new species of *Illex* from the western Atlantic and distributional aspects of other *Illex* species (Cephalopoda: Oegopsida). Proc. Biol. Soc. Wash. 82:295-322.

ROPER, C. F. E., AND R. E. YOUNG.
1975. Vertical distribution of pelagic cephalopods. Smithson. Contrib. Zool. 209, 51 p.

SCOTT, W. B., AND S. N. TIBBO.
1968. Food and feeding habits of swordfish, *Xiphias gladius*, in the western north Atlantic. J. Fish. Res. Board Can. 25:903-919.

THORE, S.
1949. Investigations on the "Dana" Octopoda. Part I. Bolitaenidae Amphitretidae, Vitreledonellidae, and Alloposidae. Dana-Rep. Carlsberg Found. 6(33), 85 p.

TIBBO, S. N., L. R. DAY, AND W. F. DOUCET.
1961. The swordfish (*Xiphias gladius* L.), its life-history and economic importance in the northwest Atlantic. Fish. Res. Board Can., Bull. 130, 47 p.

VOSS, G. L.
1953. A contribution to the life history and biology of the sailfish, *Istiophorus americanus* Cuv. and Val., in Florida waters. Bull. Mar. Sci. Gulf Caribb. 3:206-240.
1967. The biology and bathymetric distribution of deep-sea cephalopods. Stud. Trop. Oceanogr. (Miami) 5:511-535.
1973. Cephalopod resources of the world. FAO Fish. Circ. 149, 75 p.

VOSS, G. L., AND D. S. ERDMAN.
1959. *Thysanoteuthis rhombus*, large cephalopod new to the western Atlantic. Nautilus 73:23-25.

YABE, H., S. UEYANAGI, S. KIKAWA, AND H. WATANABE.
1959. Study on the life-history of the sword-fish, *Xiphias gladius* Linnaeus. [In Jpn., Engl. summ.] Rep. Nankai Reg. Fish. Res. Lab. 10:107-150.

APPENDIX TABLE 1.—Swordfish collection data.

Fish no.	Date landed	Sex[1]	Lower jaw fork length (cm)	Weight (kg)	Method of capture[2]	Hookup time (e.s.t)	Fish no.	Date landed	Sex[1]	Lower jaw fork length (cm)	Weight (kg)	Method of capture[2]	Hookup time (e.s.t)
1	17 June 1978	M	138	30	R	—	34	20 July 1978	M	170	72	R	0400
2	17 June 1978	M	142	35	R	—	35	20 July 1978	M	178	77	R	2238
3	21 June 1978	M	142	29	R	0006	36	21 July 1978	M	134	30	R	0320
4	21 June 1978	M	155	45	R	0152	37	21 July 1978	M	156	47	R	0220
5	21 June 1978	M	167	62	R	0300	38	21 July 1978	M	169	59	R	2200
6	21 June 1978	M	176	69	R	0045	39	21 July 1978	M	170	65	R	2230
7	21 June 1978	M	196	102	R	0500	40	21 July 1978	M	174	74	R	0147
8	21 June 1978	F	205	120	R	2300	41	21 July 1978	F	211	136	R	0255
9	21 June 1978	M	206	101	R	0050	42	27 July 1978	M	153	[3]45	LL	—
10	22 June 1978	M	134	29	R	0315	43	27 July 1978	M	199	[3]101	LL	—
11	22 June 1978	M	142	35	R	2230	44	13 Sept. 1978	M	138	[3]33	LL	—
12	22 June 1978	M	151	41	R	0400	45	29 Sept. 1978	M	101	[3]13	LL	—
13	23 June 1978	M	189	80	R	0246	46	29 Sept. 1978	M	165	[3]57	LL	—
14	23 June 1978	F	214	126	R	0435	47	29 Sept. 1978	M	235?	[4]166	LL	—
15	24 June 1978	M	147	41	R	0530	48	30 Sept. 1978	F	106	[3]12	LL	—
16	24 June 1978	M	193	92	R	2400	49	30 Sept. 1978	M	169	[3]61	LL	—
17	24 June 1978	M	206	112	R	0430	50	5 Oct. 1978	F	102	[3]11	LL	—
18	24 June 1978	F	207	105	R	—	51	5 Oct. 1978	M	143	[3]37	LL	—
19	24 June 1978	F	209	118	R	—	52	5 Oct. 1978	M	150	[3]42	LL	—
20	17 July 1978	M	141	36	R	0150	53	6 Feb. 1979	F	121	[3]19	LL	—
21	17 July 1978	M	160	52	R	0243	54	7 Mar. 1979	F	241	[4]203	LL	—
22	17 July 1978	M	175	64	R	2312	55	10 Apr. 1979	M	126	[3]25	LL	—
23	17 July 1978	M	181	77	R	2345	56	10 Apr. 1979	F	131	[3]25	LL	—
24	17 July 1978	M	186	72	R	2304	57	10 Apr. 1979	F	132	[3]26	LL	—
25	17 July 1978	F	213	143	R	2207	58	10 Apr. 1979	M	157	[3]49	LL	—
26	18 July 1978	—	118	20	R	0345	59	10 Apr. 1979	M	163	[3]55	LL	—
27	18 July 1978	M	158	50	R	2251	60	11 Apr. 1979	M	165	[3]57	LL	—
28	18 July 1978	M	200	110	R	—	61	6 June 1979	M	155	[3]47	LL	—
29	18 July 1978	M	209	115	R	2400	62	29 Sept. 1979	F	106	[3]12	LL	—
30	18 July 1978	M	214	125	R	0315	63	29 Sept. 1979	M	174	[3]67	LL	—
31	18 July 1978	M	218	114	R	2300	64	5 Oct. 1979	M	124	[3]24	LL	—
32	20 July 1978	M	132	27	R	0112	65	—	—	—	—	—	—
33	20 July 1978	M	140	39	R	0410							

[1]M = Male, F = Female.
[2]R = Rod and reel, LL = Longline.
[3]Weight computed from weight/length formulas according to sex (Southeast Fisheries Center text footnote 3).
[4]Weight computed from dressed weight/whole weight formula (South Atlantic Fishery Management Council. 1980. Draft Swordfish Management Plan. Unpubl. manuscr.)

TROPHIC RELATIONSHIPS AMONG DEMERSAL FISHES IN A COASTAL AREA OF THE GULF OF MAINE[1]

JOHN S. HACUNDA[2]

ABSTRACT

Food resource utilization was investigated among eight demersal fish species (longhorn sculpin, *Myoxocephalus octodecemspinosus*; winter flounder, *Pseudopleuronectes americanus*; windowpane, *Scopthalmus aquosus*; yellowtail flounder, *Limanda ferruginea*; little skate, *Raja erinacea*; Atlantic cod, *Gadus morhua*; red hake, *Urophycis chuss*; ocean pout, *Macrozoarces americanus*) over a 13-month period in an area of Johns Bay, Maine. Despite the dominance of polychaetes and mollusks in the benthos, crustaceans composed the major prey group in all predators. There was considerable trophic similarity among the fishes and the amphipods *Unciola* sp. and *Leptocheirus pinguis* were the most important prey in seven of the eight predators. The results indicate that resource partitioning by prey size is related to different mouth morphologies for closely related species (winter flounder, yellowtail flounder, windowpane), and that unrelated species with similar mouth morphologies may overlap in prey size use (longhorn sculpin, Atlantic cod).

Recent studies have revealed the complexity of feeding relations among marine organisms (Isaacs 1972; Lange and Hurley 1975). The concept of unstructured food webs necessitates a detailed knowledge of the food habits of component species in order to establish their trophic connections and to determine energy flow pathways through the ecosystem. Fish food habit studies are helpful in deciphering some of the higher level trophic relations in an ecosystem. From a practical standpoint, information on the quantity and quality of food consumed by fish is needed for estimating fish production (Paloheimo and Dickie 1970; Mills and Fournier 1979). In addition, knowledge of the feeding ecology of noncommercial, as well as commercial species, is essential for implementing a multispecies approach to fishery management (Gulland 1977; Larkin 1978).

Studies of the food habits of fish communities in the marine environment are becoming increasingly popular. Most of the early effort was centered on freshwater fish communities (e.g., Nilsson 1967; Keast 1970; Zaret and Rand 1971), but there is now a growing literature on marine systems (e.g., Tyler 1972; Hobson and Chess 1976; Kislalioglu and Gibson 1977; Langton and Bowman 1980; Hunter[3]). These fish population studies are part of a broader area of research in modern ecology concerned with the question of how closely related species coexist in communities. Patterns of resource utilization by cooccurring species have been studied to assess interspecific competition and gain insight into community organization (see review by Schoener 1974).

The purpose of the present study is to examine feeding relationships among demersal fishes in a coastal area of the Gulf of Maine. Specifically, the objectives are 1) to determine quantitatively the principal prey species of the demersal fishes, 2) to examine food resource division and interrelationships among the predator species, and 3) to compare predator diets with food resources potentially available in the benthic infauna.

METHODS

I made monthly trawl collections of demersal fishes in Johns Bay, Maine, from April 1978 through April 1979. A 5.5 m otter trawl was used during the initial 3 mo of sampling. For the remainder of the study I used a 9.1 m otter trawl. The trawl had a 50.8 mm #15 nylon mesh with a 38.1 mm cod end. Trawls were made in approximately

[1]Contribution No. 151, Ira C. Darling Center, University of Maine at Orono, Walpole, ME 04573.
[2]Graduate School of Oceanography, University of Rhode Island, Kingston, RI 02881.

Manuscript accepted June 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

[3]Hunter, M. 1979. Food resource partitioning by demersal fishes from the vicinity of Kodiak Island, Alaska. *In* S. J. Lipovsky and C. A. Simenstad (editors), Fish food habits studies (Proc. 2d Pac. NW. Tech. Workshop), p. 179-186. Wash. Sea Grant Publ. WSG-WO-79-1.

30 m of water along the eastern side of Johns Bay (Figure 1). Two or three 15-min trawls were made during each sampling trip to obtain a sufficient number of fish. I measured temperature and salinity at the surface (1 m and at a depth of 30 m) using a Beckman[4] RS5-3 salinometer.

Immediately after capture I sorted the trawl catch by species. Total length (TL to nearest millimeter), weight (to nearest gram), sex, and maturity determinations were made for each specimen. By cutting at the esophagus and pyloric constriction stomachs were removed from a maximum of 20 specimens (>15 cm TL) of each species (a subsample of the total size range), fixed in 10% Formalin, later preserved in 70% isopropanol, and then, contents were sorted and identified to the lowest possible taxon. Prey items were damp dried on bibulous paper, and the number of individuals and total wet weight (to nearest 0.01 g) of each prey category were recorded. Total weight included shell weight for mollusks, crustaceans, and echinoderms.

I determined the contribution of different prey categories to the diet of a fish species by three methods: 1) the percentage weight of a prey category (pooled) to the weight of the total stomach contents, 2) the percentage abundance of individuals of a prey category to the total number of individual prey in the stomachs, and 3) the percentage frequency of occurrence of the number of stomachs in which a prey category occurred to the total number of stomachs examined. Berg (1979) discussed the limitations of using any single measure to evaluate the importance of a food taxon. Therefore, an index of relative importance, modified from Pinkas et al. (1971), has been calculated since it incorporates all three measures and gives a better assessment of the dietary importance of a prey group. The formula used is as follows: $IRI = (N + W)F$, where N = numerical percentage, W = weight percentage, F = percentage frequency of occurrence, and IRI = index of relative importance. The original formulation proposed by Pinkas et al. (1971) used volumetric percentage instead of percentage weight.

I calculated niche overlap using the formula proposed by Pianka (1973):

$$A_{ij} = \frac{[\Sigma p_{ih} p_{jh}]}{[\Sigma p^2_{ih}\ \Sigma p^2_{jh}]}$$

where A_{ij} is the overlap of species j on species i; p_{ih} is the proportion (percentage weight) of a particular food h ($h = 1\ldots,s$) in the diet of species i; and p_{jh} is the proportion of the same food h in the diet of species j. Values for the overlap index may vary between 0, if no overlap occurs, and 1 for complete overlap. A value >0.3 is significant and ones >0.7 are considered high (Keast 1978).

The division of principal prey among the predators was examined by means of a partition plot. I defined principal prey as those with an IRI >100 because this emphasized the major food sources of each predator. Principal prey accounted for 73.3-94.7% by number of the food items in predator diets. The partition plot facilitates the calculation of the percentage reoccurrence of prey in more than one predator, which is empirically defined as the number of reoccurrences observed divided by the total number of reoccurrences possible in the plot, multiplied by 100 (Tyler 1972). One reoccurrence is defined as the presence of a prey in two

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

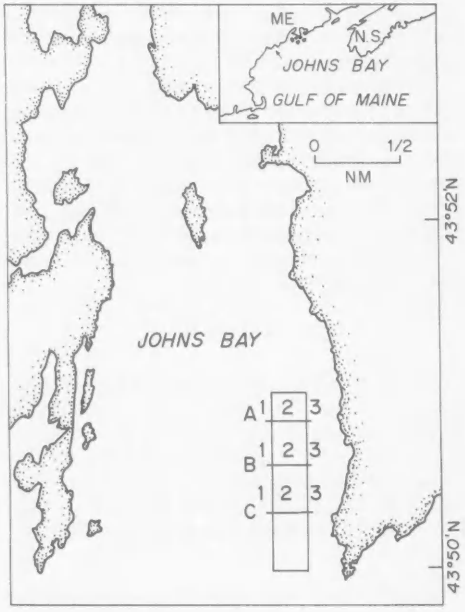

FIGURE 1.—Location of trawling area (closed box) and benthic sampling sites (transects A-C, stations 1-3) in Johns Bay, Maine.

predators. The total number of reoccurrences possible is obtained by the number of predators minus one, multiplied by the number of prey. The percentage reoccurrence of principal prey was calculated a second way by modifying the above procedure and ranking the principal prey in each predator's diet in terms of relative importance (e.g., first = 4 points, second = 3 points, third = 2 points, fourth = 1 point, each additional principal prey = ½ point). In this case, points are totaled for principal prey that are shared by two or more predators, and this value is divided by the total points possible if complete overlap occurred for all principal prey in all predators, the result being multiplied by 100 to give a percentage.

I made length measurements of crustacean prey species for several predators according to the procedure used by Ross (1977). A sample ($N \leq 25$) of each principal prey species was measured for several specimens of each predator. Measurements were made to the nearest millimeter along the axis of greatest dimension. Mouth measurements of fish species were also taken to compare prey size with mouth morphology. Upper jaw length was the distance from the posterior end of the maxillary to the tip of the snout. Mouth width was the distance between the posterior edges of the maxillaries with the mouth fully closed.

I collected benthic samples in September using a ponar grab. A series of three transects was established along the trawl tract (Figure 1). Three stations at different depths were sampled along each transect. Each ponar grab sampled a 0.05 m^2 area. Samples were washed through a 0.5 mm sieve and then fixed in 10% Formalin. I analyzed grab samples in the same manner as the stomach contents.

RESULTS

Abundance of Fishes

Twenty species of fish were collected during the 13-mo sampling period. The most abundant species were the longhorn sculpin, *Myoxocephalus octodecemspinosus*, and the winter flounder, *Pseudopleuronectes americanus*. The fish community showed the greatest diversity and abundance during summer. From January to March the fish fauna was limited and no fish at all were taken in the February sample.

The fish community can be broken down into different temporal components (Tyler 1971). "Regulars" were those species present on nearly every sampling date and included the longhorn sculpin; winter flounder; yellowtail flounder, *Limanda ferruginea*; and the Atlantic cod, *Gadus morhua*. "Summer periodics" were those species found in samples taken during the warmer months: the windowpane, *Scopthalmus aquosus*; ocean pout, *Macrozoarces americanus*; red hake, *Urophycis chuss*; and little skate, *Raja erinacea*. There was no corresponding "winter periodics" group. "Occasionals" were fish that occurred in low numbers at infrequent intervals: the sea raven, *Hemitripterus americanus*; the winter skate, *R. ocellata*; thorny skate, *R. radiata*; American plaice, *Hippoglossoides platessoides*; fourspotted flounder, *Paralichthys oblongus*; witch flounder, *Glyptocephalus cynoglossus*; cunner, *Tautogolabrus adspersus*; silver hake, *Merluccius bilinearis*; white hake, *Urophycis tenuis*; alligatorfish, *Aspidophoroides monopterygius*; moustache sculpin, *Triglops murrayi*; and sand lance, *Ammodytes* sp.

Foods

I examined the foods of the eight most abundant species (longhorn sculpin, winter flounder, windowpane, yellowtail flounder, ocean pout, little skate, Atlantic cod, and red hake). The diet for each species for the entire sampling period is summarized in Tables 1-8.

Longhorn Sculpin

Sixty-three prey taxa were identified in the 299 longhorn sculpin stomachs. Crustaceans were the most important prey group, making up 58.4% of the diet by weight and 95.8% of the diet by number (Table 1). Amphipods were most heavily preyed upon, especially *Unciola* sp. and *Leptocheirus pinguis*, which had the two highest indices of relative importance. Decapods were next in importance, with the sand shrimp, *Crangon septemspinosa*, and rock crab, *Cancer irroratus*, constituting 18.2% of the diet by weight. Mysids, principally *Mysis mixta*, were also significant food items. Pisces were the second major prey group and made up 25.2% of the diet by weight. Larval Atlantic herring, *Clupea harengus harengus*, were important fish prey. Other phyla (Porifera, Polychaeta, Mollusca) formed a minor portion of the diet.

TABLE 1.—Stomach contents of 299 longhorn sculpins ranging from 15.8 to 32.2 cm TL (mean 21.1 ± 3.4 cm) and 21 to 380 g (mean 101 ± 52 g). Twenty-four stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			
	Weight	Number	Frequency[1]	*IRI*
Porifera total	0.00	0.02	0.33	0
Polychaeta total	2.92	1.08	19.40	78
Mollusca total	.34	.61	7.69	7
Crustacea total	58.42	95.84	88.63	13,672
Mysidacea total	3.55	10.26	29.10	402
Neomysis americana	1.23	4.11	7.69	41
Mysis mixta	1.79	4.80	14.72	97
Other Mysidacea	.53	1.35		
Cumacea total	.04	.32	4.01	1
Isopoda total	1.50	2.55	13.38	54
Edotea montosa	.17	1.96	8.70	19
Cirolana sp.	1.33	.59	5.35	10
Amphipoda total	25.66	78.94	82.61	8,641
Unciola sp.	10.58	46.64	64.55	3,694
Leptocheirus pinguis	10.21	16.94	40.47	1,099
Aeginella longicornis	1.12	6.22	25.08	184
Erichthonius rubricornis	.20	3.09	14.72	48
Hippomedon serratus	.30	1.32	8.36	14
Monoculodes sp.	.13	.95	10.70	12
Other Amphipoda	3.12	3.78		
Decapoda total	27.67	3.77	30.77	967
Crangon septemspinosa	10.05	2.06	14.72	178
Cancer irroratus	8.15	.71	6.69	59
Other Decapoda	9.47	1.00		
Pisces total	25.19	2.45	18.39	508
Clupea h. harengus	11.04	2.01	10.03	131
Other Pisces	14.15	.44		
Remains	11.16			
Detritus	1.97			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

TABLE 2.—Stomach contents of 201 winter flounder ranging from 15.2 to 42.6 cm (mean 24.0 ± 6.0 cm) and 29 to 1,120 g (mean 209 ± 187 g). Fifty-seven stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			
	Weight	Number	Frequency[1]	*IRI*
Nemertea total	0.16	0.05	0.50	0
Algae total	12.67	0	2.49	32
Polychaeta total	18.26	8.11	53.73	1,417
Phyllodoce sp.	.28	2.19	20.90	52
Melinna cristata	2.16	2.19	4.48	19
Maldanidae	.69	.80	9.95	15
Lumbrineris fragilis	2.79	.53	6.97	23
Pherusa affinis	5.03	.42	5.47	30
Other Polychaeta	7.31	1.98		
Mollusca total	6.09	3.13	24.88	229
Bivalvia total	5.13	2.60	22.89	177
Cerastoderma pinnulatum	4.21	1.87	17.91	109
Other Bivalvia	.92	.73		
Gastropoda total	.96	.53	3.98	6
Crustacea total	32.50	86.72	70.65	8,422
Cumacea total	1.02	3.99	27.36	137
Diastylis quadrispinosa	.50	1.87	14.43	34
Other Cumacea	.52	2.12		
Isopoda total	.20	.58	6.97	5
Edotea montosa	.15	.47	5.97	4
Other Isopoda	.05	.11		
Amphipoda total	25.74	81.96	69.65	7,502
Ampelisca agassizi	.49	7.09	9.45	72
Leptocheirus pinguis	9.18	16.24	32.34	822
Corophium sp.	.11	1.77	10.95	21
Erichthonius rubricornis	.01	1.37	13.44	17
Unciola sp.	10.17	44.30	56.22	3,062
Pontogeneia inermis	.29	.76	4.98	5
Aeginella longicornis	2.86	6.94	16.92	166
Other Amphipoda	2.63	3.49		
Decapoda total	5.53	.18	3.98	23
Echinodermata total	.50	1.98	24.38	62
Ophiuroidea total	.39	1.87		52
Amphipholis squamata	.16	.92	11.94	13
Other Ophiuroidea	.23	.95		
Asteroidea total	0	.03	.50	0
Echinoidea total	.11	.08	1.49	0
Remains	15.03			
Detritus	14.81			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Winter Flounder

Sixty-six prey taxa were identified from the 201 winter flounder stomachs. Crustaceans were the major prey group for the winter flounder (Table 2). Amphipods accounted for the largest percentage of the diet by weight (25.7%). *Unciola* sp., *Leptocheirus pinguis*, and *Aeginella longicornis* were the principal amphipods consumed. Cumaceans, isopods, and decapods were of minor importance. After crustaceans, polychaetes were the next major prey group, making up 18.3% of the diet by weight. Polychaete identification was often difficult due to partial digestion or incomplete animals and this obscured the importance of some species. *Melinna cristata, Lumbrineris fragilis, Pherusa affinis*, and *Phyllodoce* sp. were the principal polychaetes consumed. Mollusks were of little importance, but one species, the bivalve *Cerastoderma pinnulatum*, was preyed on significantly and constituted 4.2% of the diet by weight. Algae made up 12.7% of the diet. Echinoderms accounted for only a small fraction of the stomach contents.

Windowpane

The windowpane had a specialized diet and only seven prey taxa were found in the 37 stomachs. Crustaceans were by far the most important prey group, constituting 79.3% of the diet by weight and 99.0% of the diet by number (Table 3). Mysids, principally *Mysis mixta*, were the main component of the crustacean prey. *Mysis mixta* accounted for 72.4% of the diet by weight. Pisces, namely *Clupea h. harengus*, were secondary in importance and made up 20.3% of the diet by weight. Polychaetes composed a negligible portion of the diet.

Yellowtail Flounder

The 60 yellowtail flounder stomachs analyzed contained 39 prey taxa. Crustacea accounted for

TABLE 3.—Stomach contents of 37 windowpane ranging from 21.0 to 33.6 cm (mean 27.3±3.3 cm) and 90 to 482 g (mean 244±90 g). Eight stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			
	Weight	Number	Frequency[1]	*IRI*
Polychaeta total	0.13	0.06	2.70	1
Crustacea total	79.27	98.99	75.68	13,490
Mysidacea total	78.78	98.74	75.68	13,434
Neomysis americana	1.16	2.46	8.11	29
Mysis mixta	72.41	94.65	59.46	9,933
Other Mysidacea	5.21	1.63		
Amphipoda total	.26	.19	8.11	4
Decapod total	.23	.06	2.70	1
Pisces *Clupea h. harengus*	20.25	0.94	2.70	57
Remains	0.36			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

almost half the diet by weight (48.5%) and almost the entire diet by number (95.1%) (Table 4). Amphipods were the most important crustaceans consumed, followed by mysids, cumaceans, and decapods. *Unciola* sp. was the principal amphipod prey, making up 28.7% of the diet by weight and 82.0% of the diet by number. The amphipod *Leptocheirus pinguis* and mysid *Mysis mixta* were also important. After crustacea, polychaetes (10.2% of the diet by weight) and mollusks (5.2% of the diet by weight) were the next largest dietary components. The bivalve *Cerastoderma pinnulatum* was a significant prey item. Other prey groups (Nemertea, Echinodermata, Pisces) were of minor importance.

TABLE 4.—Stomach contents of 60 yellowtail flounder ranging from 19.0 to 42.0 cm (mean 30.9±7.2 cm) and 42-670 g (mean 280±174 g). Fourteen stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			
	Weight	Number	Frequency[1]	*IRI*
Nemertea total	3.50	0.00	1.67	6
Polychaeta total	10.15	2.38	35.00	438
Phyllodoce sp.	.32	.40	10.00	7
Nephtys sp.	2.64	.04	3.33	9
Glycera sp.	.23	.18	5.00	2
Maldanidae	.87	.44	11.67	15
Other Polychaeta	6.09	1.32		
Mollusca total	5.19	2.33	36.67	276
Bivalvia total	5.19	2.29	36.67	274
Nucula proxima	1.46	.63	5.00	10
Cerastoderma pinnulatum	3.41	1.44	26.67	129
Other Bivalvia	.32	0.22		
Gastropoda total	0	.04	1.67	0
Crustacea total	48.50	95.07	68.33	9,810
Cumacea total	.45	1.57	21.67	44
Diastylis quadrispinosa	.23	.36	8.33	5
Other Cumacea	.22	1.21		
Amphipoda total	33.58	85.78	63.33	7,559
Leptocheirus pinguis	1.73	.99	25.00	68
Unciola sp.	28.66	82.01	53.33	5,903
Hippomedon serratus	.27	.49	11.67	9
Monoculodes sp.	.41	.72	13.33	15
Other Amphipoda	2.51	1.57		
Mysidacea total	12.51	7.27	3.33	66
Mysis mixta	12.19	7.18	3.33	65
Other Mysidacea	.32	.09		
Decapoda *Crangon septemspinosa*	1.59	.13	5.00	9
Isopoda total	.37	.32	8.33	6
Echinodermata total	.05	.13	6.67	1
Pisces total	.05	.04	1.67	0
Remains	16.38			
Detritus	16.20			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Ocean Pout

Twenty-seven prey taxa were found in the 46 ocean pout stomachs. A comparison of the relative contributions of echinoderms and crustaceans to the diet showed that echinoderms were the most important prey group in terms of percent weight (20.6% vs. 13.7%), while crustaceans had a greater *IRI* (7,382 vs. 974) (Table 5). Amphipods and, to a lesser extent, cumaceans were the principal crustacean orders present in the ocean pout diet. The amphipods *Unciola* sp. and *Leptocheirus pinguis* and the cumacean *Diastylis quadrispinosa* were significant prey. Principal echinoderm prey were the sea urchin, *Strongylocentrotus droebachiensis*; the sand dollar, *Echinarachnius parma*; and

TABLE 5.—Stomach contents of 46 ocean pout ranging from 18.2 to 49.0 cm (mean 34.3±5.9 cm) and 24 to 660 g (mean 214±11.8 g). Five stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			
	Weight	Number	Frequency[1]	*IRI*
Polychaeta total	1.41	0.27	19.57	33
Mollusca total	9.78	12.11	45.65	999
Gastropoda total	.21	.45	13.04	9
Bivalvia total	9.57	11.66	39.13	831
Placopecten magellanicus	4.57	.81	4.35	23
Cerastoderma pinnulatum	3.85	4.88	21.74	190
Mya arenaria	.91	5.33	8.70	54
Other Bivalvia	.24	.64		
Crustacea total	13.65	83.37	76.09	7,382
Mysidacea total	.14	.27	4.35	2
Cumacea total	2.12	18.78	41.30	863
Diastylis quadrispinosa	1.86	15.90	26.09	453
Other Cumacea	.26	2.88		
Isopoda *Edotea montosa*	.02	.36	6.52	2
Amphipoda total	10.29	63.32	71.74	5,281
Leptocheirus pinguis	1.15	2.71	17.39	67
Unciola sp.	8.00	57.99	58.70	3,874
Pontogenia inermis	.09	.91	6.52	7
Aeginella longicornis	.07	.54	6.52	4
Other Amphipoda	.98	1.17		
Decapoda total	1.08	.54	10.87	19
Echinodermata total	20.63	4.25	39.13	974
Echinoidea total	19.81	1.35	23.91	506
Strongylocentrotus drobachiensus	1.78	.99	15.22	42
Echinarachnius parma	18.03	.36	10.87	200
Ophiuroidea total	.82	2.90	26.09	97
Amphipholis squamata	.40	2.18	15.22	39
Other Ophiuroidea	.42	.72		
Detritus	47.55			
Remains	6.99			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

the brittle star, *Amphipholis squamata*. Mollusca constituted 9.8% of the diet by weight. The sea scallop, *Placopecten magellanicus*; the soft-shell clam, *Mya arenaria*; and the cockle, *Cerastoderma pinnulatum*, were noteworthy. Polychaetes formed a small portion of the diet. A large amount of bottom sediment and organic material was found in the stomachs examined.

Little Skate

Thirty-one prey taxa were found in the 33 little skate stomachs. The little skate fed primarily on crustaceans (Table 6). The decapods were the most important group, making up 50.7% of the diet by weight. *Crangon septemspinosa* and *Cancer irroratus* were principal prey species. Amphipods were next in importance with *L. pinguis*, *Unciola* sp., and *Monoculodes* sp. as significant prey items. The remaining crustacean groups did not constitute a substantial part of the diet. Polychaetes were the next major prey group, accounting for 10.1% of the diet by weight. Porifera, Nematoda, and Pisces were of minor importance.

TABLE 6.—Stomach contents of 33 little skates ranging from 25.6 to 55.2 cm (mean 39.6 ± 10.1 cm) and 71 to 1,194 g (mean 496 ± 346 g). There were no empty stomachs. *IRI* = index of relative importance (see text).

Taxon	Percentage			*IRI*
	Weight	Number	Frequency[1]	
Porifera total	0.15	0.00	3.03	0
Nematoda total	.08	4.17	15.15	64
Polychaeta total	10.14	.17	36.36	375
Crustacea total	66.89	94.78	96.97	15,677
Mysidacea total	.19	1.22		
Mysis mixta	.13	.70	6.06	5
Other Mysidacea	.06	.52		
Cumacea total	.08	1.22	15.15	20
Amphipoda total	15.80	70.78	84.85	7,347
Ampelisca agassizi	.06	1.04	9.09	10
Leptocheirus pinguis	5.01	24.17	66.67	1,946
Unciola sp.	1.37	12.52	51.52	716
Pontogenia inermis	.08	1.57	12.12	20
Anonyx sarsi	2.38	3.13	9.09	50
Monoculodes sp.	2.42	24.52	57.58	1,551
Other Amphipoda	4.48	3.83		
Decapoda total	50.71	21.39	78.79	5,680
Crangon septemspinosa	18.51	9.22	57.58	1,596
Cancer irroratus	22.68	9.39	36.36	1,166
Other Decapoda	9.52	2.78		
Isopoda total	.11	.17	3.03	1
Pisces total	.67	.87	15.15	23
Detritus	1.60			
Remains	20.47			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Atlantic Cod

The 75 Atlantic cod stomachs contained a total of 30 prey taxa. Crustaceans were the major prey group, accounting for 40.3% of the diet by weight and 98.5% of the diet by number (Table 7). Amphipods, especially *Unciola* sp. and *L. pinguis*, were most heavily preyed upon. The decapods made up 18.2% of the diet by weight, with *Crangon septemspinosa* and *Cancer irroratus* as principal prey. The mysids, notably *Mysis mixta*, were next in importance. Cumaceans and isopods made up a negligible portion of the diet. Pisces were the next major group and constituted 14.6% of the diet by weight. Other phyla (Nematoda, Polychaeta, Mollusca, and Echinodermata) were of little importance. A large amount of unidentifiable remains (40.9% of the diet by weight) was found in the stomachs examined.

TABLE 7.—Stomach contents of 75 Atlantic cod ranging from 15.0 to 53.6 cm (mean 22.5 ± 5.5 cm) and 27 to 1,555 g (mean 128 ± 195 g). Ten stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			*IRI*
	Weight	Number	Frequency[1]	
Nematoda total	0.00	0.35	4.00	1
Polychaeta total	1.06	.35	12.00	17
Mollusca total	.02	.43	1.33	1
Crustacea total	40.27	98.45	84.00	11,652
Mysidacea total	4.00	8.46	38.67	481
Mysis mixta	2.45	7.42	25.33	250
Other Mysidacea	1.55	1.04		
Cumacea total	.07	1.04	5.33	6
Isopoda total	1.01	.43	5.33	8
Cirolana polita	1.01	.35	4.00	5
Other Isopoda	.00	.08		
Amphipoda total	16.98	85.85	72.00	7,404
Ampelisca agassizi	.51	10.01	2.67	28
Leptocheirus pinguis	2.44	3.80	21.33	133
Unciola sp.	11.16	66.01	58.67	4,528
Pontogenia inermis	.12	1.21	10.67	14
Hippomedon serratus	.45	1.55	12.00	24
Aeginella longicornis	.05	.69	6.67	5
Other Amphipoda	2.25	2.58		
Decapoda total	18.21	2.67	24.00	501
Crangon septemspinosa	9.06	1.55	13.33	141
Cancer irroratus	6.07	.26	4.00	25
Other Decapoda	3.08	.86		
Echinodermata total	1.94	.17	1.33	3
Pisces total	14.61	.26	5.33	79
Detritus	1.17			
Remains	40.94			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Red Hake

Twenty-four prey taxa were found in the 30 red hake stomachs. The red hake fed principally upon crustaceans, and this group accounted for 72.4% of the diet by weight (Table 8). Amphipods were the most important order with *L. pinguis*, *Unciola* sp., and *Ampelisca agassizi* as significant prey items. Decapods were also heavily preyed upon and

Crangon septemspinosa was a principal prey species. Mysids, cumaceans, and isopods were of minor importance. Other groups (Algae, Porifera, Polychaeta, Mollusca) constituted a small portion of the diet.

TABLE 8.—Stomach contents of 30 red hake ranging from 15.0 to 40.1 cm (mean 25.6 ± 6.1 cm) and 22 to 392 g (mean 121 ± 86 g). Three stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage			*IRI*
	Weight	Number	Frequency[1]	
Algae total	1.60	0.00	3.33	5
Porifera total	.16	0.00	3.33	1
Polychaeta total	3.35	.63	20.00	80
Crustacea total	72.36	99.36	86.67	14,884
Mysidacea total	.24	.31	3.33	2
Cumacea total	.16	2.19	13.33	31
Isopoda total	3.19	.94	10.00	41
Cirolana polita	2.96	.63	6.67	24
Other Isopoda	.23	.31		
Amphipoda total	31.87	87.46	80.00	9,546
Ampelisca agassizi	2.48	28.53	10.00	310
Leptocheirus pinguis	13.98	26.65	50.00	2,031
Unciola sp.	6.71	21.94	60.00	1,719
Hippomedon serratus	1.44	4.08	13.33	74
Aeginella longicornis	.32	2.19	16.67	42
Other Amphipoda	6.94	4.07		
Decapoda total	36.90	8.46	40.00	1,815
Crangon septemspinosa	28.67	7.21	26.67	957
Other Decapoda	8.23	1.25		
Mollusca total	.16	0.00	3.33	1
Detritus	.88			
Remains	21.49			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Dietary Overlap

The fish community in Johns Bay showed a considerable degree of food overlap (Table 9). Eight species-pairs had overlap values >0.50. This is a reflection of the dominance of crustaceans in the diets of the predators examined. The greatest dietary overlap occurred between the Atlantic cod and longhorn sculpin. In addition, high dietary overlaps occurred among the Atlantic cod, red hake, longhorn sculpin, little skate, winter flounder, and yellowtail flounder, a consequence of the dependence of these predators on amphipod and decapod prey.

Although over 100 prey taxa were found during the study, only 13 were classified as principal prey. In the partition plot predators that share principal prey are generally arranged adjacent to one another (Table 10). Difficulty in identifying digested organisms necessitated using the broad classification of Polychaeta in this partition plot. Generally, predators consumed 4 or 5 principal prey, and the percentage reoccurrence of principal

TABLE 9.—A summary of the predator feeding habits and food overlap in fishes from Johns Bay, Maine. Species pairs with overlaps 0.50 or greater are in italics.

Predator number	Predator species	Feeding habits	Predator species						
			2	3	4	5	6	7	8
1	Longhorn sculpin	Crustaceans and fish	*0.74*	*0.59*	*0.63*	0.43	0.43	0.19	0.18
2	Atlantic cod	Crustaceans and fish		.57	.62	.60	.34	.05	.13
3	Little skate	Crustaceans, particularly decapods			.58	.13	.19	.05	.01
4	Red hake	Crustaceans				.27	.36	.11	.01
5	Yellowtail flounder	Crustaceans and polychaetes					.51	.38	.36
6	Winter flounder	Crustaceans and polychaetes						.27	.01
7	Ocean pout	Mollusks, echinoderms, and crustaceans							.01
8	Windowpane	Specialist on mysids							

TABLE 10.—Partition plot of principal prey for demersal fishes in Johns Bay, Maine. Numbers listed are index of relative importance values for principal prey. Prey classifiction: (I) Infaunal, (E) Epifaunal, (N) Nektonic.

Prey	Longhorn sculpin	Atlantic cod	Red hake	Little skate	Winter flounder	Yellowtail flounder	Ocean pout	Windowpane
Unciola (I)	[1]3,694	[1]4,528	1,719	716	[1]3,062	[1]5,903	[1]3,874	—
Leptocheirus (I)	1,099	133	[1]2,031	[1]1,946	822	—	—	—
Crangon (E)	178	141	957	1,596	—	—	—	—
Polychaeta (I)	—	—	—	375	1,417	438	—	—
Cerastoderma (I)	—	—	—	—	109	129	190	—
Aeginella (E)	184	—	—	—	166	—	—	—
Mysis (N)	—	250	—	—	—	—	—	[1]9,933
Monoculodes (I)	—	—	—	1,551	—	—	—	—
Ampelisca (I)	—	—	310	—	—	—	—	—
Diastylis (I)	—	—	—	—	—	—	463	—
Cancer (E)	—	—	—	1,166	—	—	—	—
Echinarachnius (E)	—	—	—	—	—	—	200	—
Clupea (N)	131	—	—	—	—	—	—	—

[1]Indicates most important principal prey of prey of predator.

prey in more than one predator was 20% (19/96) by Tyler's (1972) method and 57% (65.5/116) by the ranked principal prey method.

Prey Size and Predator Mouth Morphology

Resource partitioning by prey size was examined for several predators by means of length-frequency distributions of crustacean prey. Crustaceans were analyzed because of their importance as a food group and because their hard external skeletons permitted reliable measurements.

A comparison of three flounder species showed that the winter flounder consumed the smallest prey (Figure 2). The majority of the winter flounder prey ranged between 4 and 10 mm long ($\overline{X} \pm 95\%$ CL = 6.8 ± 0.6). The yellowtail flounder prey lengths were bimodally distributed. In one group most prey ranged between 5 and 10 mm, while in the second they were between 14 and 17 mm ($\overline{X} \pm 95\%$ CL = 10.8 ± 1.3). The windowpane utilized the largest prey, with most ranging between 13 and 17 mm ($\overline{X} \pm 95\%$ CL = 14.4 ± 0.7).

The longhorn sculpin and Atlantic cod, were two other important crustacean predators examined. Longhorn sculpin prey showed a wide range in size (1-30 mm) (Figure 3). The largest proportion of longhorn sculpin prey was between 5 and 15 mm long ($\overline{X} \pm 95\%$ CL = 11.1 ± 0.7). The distribution of cod prey sizes was similar to that of the longhorn sculpin. Most of the cod prey were between 4 and 13 mm long ($\overline{X} \pm 95\%$ CL = 9.0 ± 0.7).

Data on mouth measurements are presented in Table 11. The basic mouth shape is given as the ratio of the mean mouth width to mean upper jaw

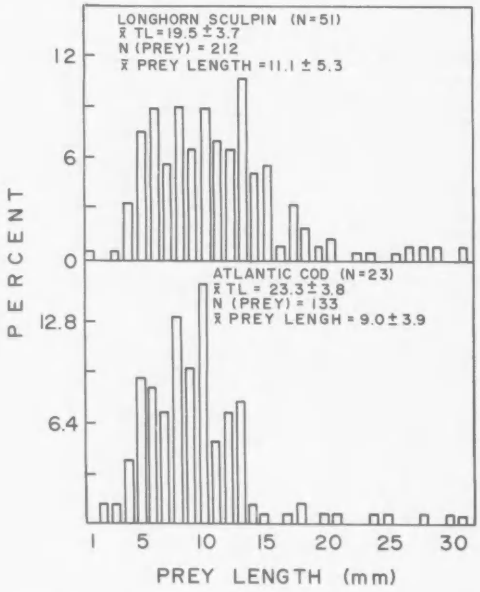

FIGURE 2.—Prey size distributions for winter flounder, yellowtail flounder, and windowpane.

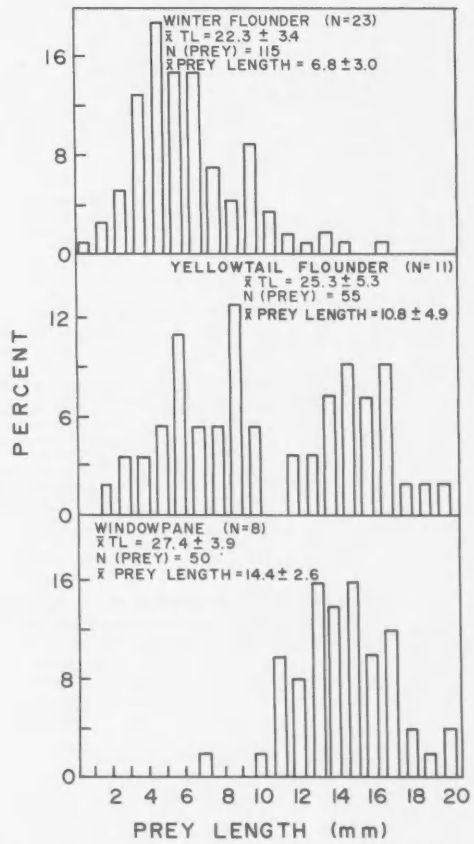

FIGURE 3.—Prey size distributions for longhorn sculpin and Atlantic cod.

TABLE 11.—Mouth dimensions of fish species.

Species	N	TL (cm) $\bar{X} \pm SD$	Upper jaw length (% TL) $\bar{X} \pm SD$	Mouth width (% TL) $\bar{X} \pm SD$	$\bar{X}$ mouth width ÷ $\bar{X}$ upper jaw length
Winter flounder	30	25.5±5.3	4.9±0.32	4.3±0.38	0.87
Yellowtail flounder	6	30.7±8.2	5.0± .39	3.8± .47	.76
Windowpane	17	24.7±4.5	9.2± .44	4.0± .80	.43
Longhorn sculpin	19	22.1±3.3	15.1± .69	16.9±1.67	1.12
Atlantic cod	3	24.5±3.1	11.7± .75	10.5± .62	1.11

length. The flounders had different ratios (windowpane 0.43, yellowtail flounder 0.76, winter flounder 0.87). The longhorn sculpin (1.12) and the Atlantic cod (1.11) had similar mouth shapes.

Benthos Analysis

A summary of the species composition by numbers and weights for the benthic samples is given in Tables 12 and 13. The sediment at stations A-1, A-2, B-1, and C-1 was silty sand, and remaining stations were sand. A total of 55 species were identified. The polychaetes were the dominant group and constituted 51.4% (by number) of the organisms present. Crustaceans (34.1%) and mollusks (12.8%) were next in abundance. The remaining groups (sipunculids(?), nematodes, echinoderms) accounted for only 1.7% of the total number of individuals. The most abundant species were the polychaetes *Prionospio steenstrupi*, *Exogone hebes*, *Tharyx acutus*, *Lumbrineris fragilis*; the crustaceans *Unciola* sp. and *Ampelisca agassizi*; and the mollusk *Nucula proxima*. In terms of biomass (percentage wet weight) mollusks (41.2%) were the most important group followed by polychaetes (41.0%) and crustaceans (8.8%). The biomass was dominated by the mollusk *N. proxima* (34.6%) and to a lesser extent by the polychaetes *L. fragilis*, *Sternaspis scutata*, and *P. steenstrupi*, and the crustaceans *A. agassizi* and *Unciola* sp.

DISCUSSION

Recent studies of temperate, coastal marine fish communities have suggested that there is considerable division of food resources among predators (Tyler 1972; Kislalioglu and Gibson 1977). Tyler (1972) examined the food utilization among demersal fishes in Passamaquoddy Bay, New Brunswick, and found relatively little overlap among diets based on the percentage reoccurrence of principal prey among predators (16% summer community; 24% winter community). In Johns Bay the percentage reoccurrence of principal prey among demersal fishes was 20% which is within the range (10-24%) that Tyler calculated for other marine communities. However, assessing dietary overlap by means of the method proposed by Tyler may be misleading because all principal prey are weighted equally in the calculation (see Methods). For example, although the percentage reoccurrence of principal prey of the fishes in Johns Bay suggests considerable resource division, a closer examination of the data reveals that seven of the eight predators rely primarily on two prey types, *Unciola* and *Leptocheirus* (Table 10). If the principal prey items in each predator's diet are weighted in terms of relative importance a more accurate evaluation of dietary overlap may be determined from the partition plot. For the demersal fishes in Johns Bay the percentage reoccurrence of ranked principal prey is 57%, which indicates that predators rely on many of the same major food sources. This conclusion is supported by the food overlap values that were obtained using Pianka's (1973) formula (Table 9).

There is insufficient information provided in Tyler's (1972) paper to evaluate the relative importance of his principal prey; however, a study by Kislalioglu and Gibson (1977) provided another source of data. These authors calculated a 14.7% reoccurrence of principal prey for shallow-water fishes from three habitats in Loch Etive, western Scotland. Food resource partitioning, however, is not as dramatic as this value would indicate because of the inclusion of five pelagic fishes in the calculation. Moreover, almost all the demersal species (13 out of 15) in Loch Etive were primarily dependent on amphipods as their most important food source (based on a points method of stomach content analysis), and among these fishes 25.7% had significant dietary overlap in terms of the proportion of different amphipod species utilized. If the percentage reoccurrence of principal prey is recalculated using weighted principal prey, the result is 56%.[5] Trophic similarity is especially evident for the fishes from the open sand-shell mud habitat (which corresponds to the habitat examined in Johns Bay) where there was significant overlap in amphipod species consumed between four of the five species examined. In Loch

[5]Resource division is not strictly comparable to Johns Bay because of the differing degrees of principal prey subdivision which may affect the result of the calculation.

TABLE 12.—Summary of the numbers of live invertebrates identified in nine benthic samples (0.05 m^2) taken from Johns Bay, Maine, in September 1978 (N = number; % = percent number). See Figure 1 for locations of transects.

Taxon	Station A-1	Station A-2	Station A-3	Station B-1	Station B-2	Station B-3	Station C-1	Station C-2	Station C-3	Total N	Total %
Mollusca:											
Nucula proxima	16	7	36	9	72	—	68	—	—	208	9.85
Mya arenaria	3	9	2	1	7	1	—	—	—	23	1.09
Cerastoderma pinnulatum	—	—	—	—	3	1	—	2	3	9	.43
Thyasira gouldi	—	—	5	1	2	—	—	—	—	8	.38
Crenella grandula	—	—	4	—	4	—	—	—	—	8	.38
Astarte undata	—	—	1	—	4	—	—	—	—	5	.24
Margarites sp.	—	—	—	—	—	—	—	—	2	2	.09
Nuculana tenuisculcata	—	1	—	—	—	—	—	—	—	1	.04
Yoldia sp.	—	—	—	1	—	—	—	—	—	1	.04
Unidentified bivalves	1	3	—	1	1	—	—	—	—	6	.28
									Total	271	12.82
Crustacea:											
Unciola sp.	—	—	—	—	—	114	2	72	190	378	17.90
Ampelisca agassizi	—	3	259	—	37	—	—	—	—	299	14.16
Aeginella longicornis	—	—	1	1	2	1	—	—	—	5	.24
Hippomedon propinquus	—	—	3	—	—	—	1	—	1	5	.24
Monoculodes sp.	—	—	—	1	1	1	—	—	—	3	.14
Petalosarsia declivis	—	—	—	—	—	—	—	1	2	3	.14
Edotea montosa	—	—	—	1	—	1	—	—	—	2	.09
Hippomedon sp.	—	1	—	—	1	—	—	—	—	2	.09
Harpinia propinqua	—	—	2	—	—	—	—	—	—	2	.09
Anonyx liljeborgi	—	—	2	—	—	—	—	—	—	2	.09
Eudorella sp.	—	—	—	1	—	—	—	—	1	2	.09
Corophium sp.	—	—	—	—	—	1	—	—	1	2	.09
Protomedeia fasciata	—	—	—	—	—	1	—	—	1	2	.09
Ampelisca macrocephala	—	—	—	—	—	—	1	1	—	2	.09
Erichthonius rubricornis	—	—	—	—	—	—	—	1	—	1	.05
Diastylis sp.	—	1	—	—	—	—	—	—	—	1	.05
D. sculpta	—	—	—	—	—	—	—	1	—	1	.05
D. quadrispinosa	—	—	1	—	—	—	—	—	—	1	.05
Leptocheirus pinguis	—	—	—	—	—	1	—	—	—	1	.05
Cyathura polita	—	—	—	—	—	—	—	—	1	1	.05
Unidentified amphipods	—	—	—	—	—	4	2	—	—	6	.28
									Total	721	34.12
Polychaeta:											
Prionospio steenstrupi	1	—	19	5	458	—	30	—	—	513	24.29
Exogone hebes	—	—	—	—	1	64	—	8	78	151	7.15
Tharyx acutus	—	14	6	7	9	12	5	2	12	67	3.17
Lumbrineris fragilis	12	16	8	3	18	—	7	—	—	64	3.03
Aricidea catherinae	14	11	—	7	—	4	2	1	16	55	2.60
Clymenella torquata	—	—	1	—	4	19	1	—	23	48	2.27
Phyllodoce mucosa	3	5	—	4	9	2	—	—	4	27	1.28
Scoloplos sp.	7	1	2	11	—	—	3	—	—	24	1.14
Ammotrypane aulogaster	—	1	5	—	15	—	—	—	—	21	.99
Scolecolepides viridis	18	—	—	—	—	—	—	—	—	18	.85
Nephtys sp.	—	3	—	—	3	—	3	4	—	13	.62
N. incisa	1	1	2	4	2	—	1	—	1	12	.57
Scalibregma inflatum	—	1	1	1	3	—	3	—	—	9	.43
Flabelligeridae	2	—	—	1	—	1	2	1	—	7	.33
Amphitrite affinis	—	—	—	—	—	3	—	—	3	6	.28
Nereis virens	—	—	—	1	4	—	—	—	—	5	.24
Phyllodoce sp.	—	—	4	—	—	—	—	—	—	4	.19
Melinna cristata	—	—	2	—	—	—	2	—	—	4	.19
Polynoidae	—	2	—	—	2	—	—	—	—	4	.19
Maldanidae	—	—	—	—	4	—	—	—	—	4	.19
Terebellides stroemi	—	—	1	—	—	—	—	—	—	1	.05
Phyllodoce maculata	—	—	—	—	1	—	—	—	—	1	.05
Sabellidae	—	—	—	—	—	1	—	—	—	1	.05
Pherusa affinis	—	—	—	—	—	—	—	—	1	1	.05
Nereis sp.	—	—	—	—	—	—	—	—	1	1	.05
Paraonis sp.	—	—	—	—	—	—	—	—	1	1	.05
Spiophanes bombyx	—	—	—	—	—	—	—	—	1	1	.05
Ampharete acutifrons	—	—	—	—	—	—	1	—	—	1	.05
Sternaspis scutata	1	5	2	2	5	—	3	2	—	20	.95
									Total	1,084	51.35
Sipuncula(?)	11	—	3	—	—	—	—	—	2	16	.76
Nematoda	—	—	—	—	—	6	—	—	11	17	.80
Echinodermata											
Amphipholis squamata	—	—	—	—	—	1	—	—	—	1	.05
Echinarachnius parma	—	—	—	—	—	—	—	—	1	1	.05
									Total	2	.10
									Grand total	2,111	99.95

TABLE 13.—Summary of the weights of live invertebrates identified in nine benthic samples ($0.05m^2$) taken from Johns Bay, Maine in September 1978 (Wt = weight in grams; % = percent weight; tr = <0.01 gram) See Figure 1 for location of transects.

Taxon	Station A-1	Station A-2	Station A-3	Station B-1	Station B-2	Station B-3	Station C-1	Station C-2	Station C-3	Total Wt	Total %
Mollusca:											
Nucula proxima	0.30	0.12	0.54	0.19	1.49	—	1.92	—	—	4.56	34.60
Mya arenaria	.03	.08	.02	.01	.14	tr	—	—	—	.28	2.12
Margarites sp.	—	—	—	—	—	—	—	—	0.14	.14	1.06
Thyasira gouldi	—	—	.03	.01	.02	—	—	—	—	.06	.46
Astarte undata	—	—	.01	—	.05	—	—	—	—	.06	.46
Crenella glandula	—	—	.02	—	.03	—	—	—	—	.05	.38
Yoldia sp.	—	—	—	.05	—	—	—	—	—	.05	.38
Nuculana tenuisculcata	—	.02	—	—	—	—	—	—	—	.02	.15
Cerastoderma pinnulatum	—	—	—	—	.03	tr	—	0.04	.04	.11	.80
Unidentified bivalves	.01	.07	—	tr	.02	—	—	—	—	.10	.76
									Total	5.43	41.20
Crustacea:											
Ampelisca agassizi	—	.01	.48	—	.05	—	—	—	—	.54	4.10
Unciola sp.	—	—	—	—	—	0.13	tr	.07	.26	.46	3.49
Monoculodes sp.	—	—	—	.01	.01	.01	—	—	—	.03	.23
Hippomedon sp.	—	.01	—	—	.02	—	—	—	tr	.03	.23
Ampelisca macrocephala	—	—	—	—	—	—	tr	.02	—	.02	.15
Hippomedon propinquus	—	—	.02	—	—	—	—	—	—	.02	.15
Leptocheirus pinguis	—	—	—	—	—	.01	—	—	—	.01	.08
Edotea montosa	—	—	—	.01	—	tr	—	—	—	.01	.08
Aeginella longicornis	—	—	tr	tr	tr	tr	—	—	—	tr	—
Erichthonius rubricornis	—	—	—	—	—	—	—	tr	—	tr	—
Harpinia propinqua	—	—	tr	—	—	—	—	—	—	tr	—
Corophium sp.	—	—	—	—	—	tr	—	—	tr	tr	—
Anonyx liljeborgi	—	—	tr	—	—	—	—	—	—	tr	—
Protomedeia fasciata	—	—	—	—	—	tr	—	—	tr	tr	—
Diastylis sp.	—	tr	—	—	—	—	—	—	—	tr	—
D. sculpta	—	—	tr	—	—	—	—	tr	—	tr	—
D. quadrispinosa	—	—	tr	—	—	—	—	—	—	tr	—
Eudorella sp.	—	—	—	tr	—	—	—	—	tr	tr	—
Petalosarsia declivis	—	—	—	—	—	—	—	tr	tr	tr	—
Cyathura polita	—	—	—	—	—	—	—	—	tr	tr	—
Unidentified amphipods	—	—	—	—	—	.03	.01	—	—	.04	.30
									Total	1.16	8.81
Polychaeta:											
Lumbrineris fragilis	.02	.12	.40	.02	.49	—	.11	—	—	1.16	8.80
Sternaspis scutata	.01	.11	.05	—	.22	—	.25	—	—	.64	4.86
Prionospio steenstrupi	tr	—	.01	tr	.48	—	.03	—	—	.52	3.95
Nephtys sp.	—	.01	—	.02	.04	—	.01	.24	.03	.35	2.66
Clymenella torquata	—	—	.03	—	.01	.11	tr	—	.15	.30	2.28
Maldanidae	—	.10	.07	—	.03	—	—	.08	—	.28	2.12
Tharyx acutus	.03	.04	.01	.03	.03	.03	.03	tr	.01	.21	1.59
N. incisa	tr	.01	.10	.03	.01	—	.03	—	.02	.20	1.52
Scoloplos sp.	.02	.02	.02	.05	.01	—	.02	—	—	.14	1.06
Scolecolepides viridis	.03	—	—	—	.11	—	—	—	—	.14	1.06
Aricidea catherinae	.02	.02	—	—	—	.01	.01	tr	.01	.07	.53
Scalibregma inflatum	—	tr	.02	—	.03	—	—	—	tr	.05	.38
Exogone hebes	—	—	—	—	tr	.02	—	.01	.03	.06	.46
Pherusa affinis	—	—	—	—	—	—	—	—	.06	.06	.46
Melinna cristata	—	—	.02	—	—	—	.03	—	—	.05	.38
Amphitrite affinis	—	—	—	—	—	.01	—	—	.03	.04	.30
Paraonis sp.	—	—	—	—	—	—	—	—	.04	.04	.30
Ammotrypane aulogaster	—	tr	tr	—	.04	—	—	—	—	.04	.30
Flabelligeridae	.01	—	—	tr	—	tr	tr	.01	—	.02	.15
Terebellides stroemi	—	—	.02	—	—	—	—	—	—	.02	.15
Sabellidae	—	—	—	—	—	.02	—	—	—	.02	.15
Ampharetes acutifrons	—	—	—	—	—	—	.02	—	—	.02	.15
Phyllodoce mucosa	tr	.01	—	tr	tr	tr	—	tr	tr	.01	.08
Phyllodoce sp.	—	—	.01	—	—	—	—	—	—	.01	.08
Polynoidae	—	.01	—	—	—	—	—	—	—	.01	.08
Phyllodoce maculata	—	—	—	—	tr	—	—	—	—	tr	—
Nereis virens	—	—	—	tr	tr	—	—	—	—	tr	—
Nereis sp.	—	—	—	—	—	—	—	—	tr	tr	—
Spiophanes bombyx	—	—	—	—	—	—	—	—	tr	tr	—
Unident. polychaetes	—	.24	.08	—	.15	.07	.18	.09	.13	.94	7.13
									Total	5.40	40.98
Nemertea:	—	.05	—	—	.25	—	.70	—	—	1.00	7.59
Sipuncula(?):	.12	—	—	—	.04	—	.03	—	—	.19	1.44
Nematoda:	—	—	—	—	—	tr	—	tr	—	tr	—
Echinodermata:											
Amphipholis squamata	—	—	—	—	—	tr	—	—	tr	tr	—
									Grand total	13.18	100.00

Etive as in Johns Bay, use of an unweighted percentage reoccurrence of principal prey to evaluate dietary overlap gives an exaggerated picture of partitioning of prey types.

Trophic partitioning by prey size was apparent for the three flounder species examined from Johns Bay (Figure 2). Keast and Webb (1966) have stressed the importance of mouth morphology and body form in channeling predators towards distinct prey. The small-mouthed winter flounder selected small crustaceans, mainly amphipods, and the larger mouthed windowpane concentrated on larger prey, primarily mysids. The yellowtail flounder had a mouth size intermediate between the other two flounder species and it fed on prey from both size ranges. Ross (1977) noticed a similar segregation of prey sizes by searobins as spatial overlap increased. Resource partitioning by prey size was at a minimum between the Atlantic cod and longhorn sculpin (Figure 3). Both of these species had a similar mouth shape and ingested prey of the same size range. The similarity of prey size utilization is reflected in the high food overlap value (0.74) for these two species. Hespenheide (1975) observed a strong correlation between prey size overlap and prey type overlap for cohabiting birds.

An analysis of the benthic infauna was made to determine potentially available food and selectivity of prey by the demersal fishes (Tables 12, 13). Availability depends not only on prey abundance, but also on the interactions of other factors, including prey size, microdistribution, capture success, and speed of movement (Griffiths 1975). Although polychaetes and mollusks dominated in the bottom sediments, crustaceans were the preferred food of the demersal fishes. Generally, predators consumed prey that were active either at the sediment surface or in the upper few centimeters of the bottom sediments. Some abundant food items, such as *Nucula proxima, Prionospio steenstrupi*, and *Exogone hebes* were not important dietary constituents. The small size of *P. steenstrupi* and *E. hebes* probably limits their selection by predators. Predation on *N. proxima* may be low because the feeding structures of some predators prevent extensive burrowing in the sediment or because of this bivalve's low caloric value. Optimal feeding strategy predicts that animals should feed on prey that give the maximum energy yield per unit time and this will govern the degree of palatability of a prey item (Schoener 1971; Emlen 1973).

Recent work by Virnstein (1977) in Chesapeake Bay concluded that infaunal densities in soft-bottom communities are predator controlled. The cropping pressure of the demersal predators checks the population growth of many prolific benthic invertebrates. The benthos in Johns Bay is subject to varying amounts of predation pressure throughout the year. During the winter, the fish community in Johns Bay was very depauperate and it is likely that many fishes moved into warmer water offshore (Edwards 1964). Many of these demersal fishes show a decrease in feeding rate as temperature drops (Tyler[6]) and the winter flounder ceased feeding during the cold months. Because of the reduced abundance and lowered metabolism of the fishes, predation on the benthos was probably at a minimum during the winter. During the warmer months there was an influx of fish species into the bay and an increase in fish diversity and abundance. Environmental conditions are favorable at this time and the food supply may be abundant enough to support the expanded fish community without competitive interactions.

The demersal fishes in Johns Bay occupy the same habitat and there is considerable spatial overlap in their foraging zones. Active predators (e.g., Atlantic cod, red hake) forage over a wider area than sedentary predators (e.g., longhorn sculpin, ocean pout). These wide-ranging species may feed in the foraging zones of several sedentary individuals. My data suggest that the benthic fishes partition food resources by selecting prey from different depth strata (microhabitats) in the environment. Predators may choose either infaunal, epifaunal, or nektonic organisms and the proportion of these prey types in the diet is a reflection of preferred foraging strata (Table 14). At one extreme are predators that feed largely on nektonic prey (e.g., windowpane), while other fishes are strongly dependent on bottom-dwelling organisms (e.g., yellowtail flounder).

The trophic similarity of the demersal fishes in this coastal community suggests that in a food-limited environment many of these predators would experience intense competition. However, establishing food limitation is a difficult task because information is lacking both on benthic production rates and the food rations required by the

[6]Tyler, A. V. 1971. Monthly changes in stomach contents of demersal fishes in Passamaquoddy Bay, N.B. Fish. Res. Board Can., Tech. Rep. 288, 114 p.

TABLE 14.—Numerical percentage of prey types in predator diets.

Predator	Nekton	Epifauna	Infauna
Windowpane	100.0	0.0	0.0
Little skate	2.1	21.4	76.5
Longhorn sculpin	12.7	10.0	77.3
Atlantic cod	8.7	3.5	87.8
Red hake	.3	10.7	89.0
Winter flounder	0	9.1	90.9
Yellowtail flounder	7.3	.3	92.4
Ocean pout	0.3	5.0	94.7

fishes. Another factor to consider is the multidimensional aspect of resource partitioning. Previous studies of fish assemblages have suggested that subtle differences of resource use along complimentary dimensions offer a possible means of reducing interspecific competition (Werner 1977; Ross 1977; Keast 1978). There is evidence that time (e.g., daily and seasonal activity patterns) and space (e.g., foraging pattern) are additional dimensions of importance influencing food utilization by the demersal fish community in Johns Bay. However, unraveling the confounding effects of resource use along several dimensions depends upon more detailed study of these cohabiting fishes as well as increased sophistication of techniques for community analysis (Pianka 1980).

ACKNOWLEDGMENTS

I wish to thank the members of my thesis committee: Hugh DeWitt, John Dearborn, Leslie Watling, and Bernard McAlice. I am grateful to Richard Langton, Northeast Fisheries Center, Woods Hole Laboratory, NMFS, NOAA, Woods Hole, Mass., for critically reading the manuscript. I am indebted to Gilbert Jaeger, Alan Hillyard, Heather Holman, Terry Cucci, and John Stewart for assistance in identifying specimens. Sincere thanks are extended to David Hodges and Margaret Hunter for their help in computer programming. I also wish to thank Jonathan Land for his conscientious laboratory work. The competent assistance of boat captain Michael Dunn is also gratefully acknowledged. Finally, special appreciation is given to David Townsend, Richard Shaw, Paul Grecay, and an anonymous reviewer for valuable discussion and comments.

LITERATURE CITED

BERG, J.
1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). Mar. Biol. (Berl.) 50:263-273.

EDWARDS, R. L.
1964. Relation of temperature to fish abundance and distribution in the Southern New England area. Int. Comm. Northwest Atl. Fish. Spec. Publ. 6:95-110.

EMLEN, J. M.
1973. Ecology: an evolutionary approach. Addison-Wesley Publ. Co., Reading, Mass., 493 p.

GRIFFITHS, D.
1975. Prey availability and the food of predators. Ecology 56:1209-1214.

GULLAND, J. A.
1977. Goals and objectives of fishery management. FAO Fish. Tech. Pap. 166, 14 p.

HESPENHEIDE, H. A.
1975. Prey characteristics and predator niche width. *In* M. L. Cody and J. M. Diamond (editors), Ecology and evolution of communities, p. 158-180. Harv. Univ. Press, Camb.

HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.

ISAACS, J. D.
1972. Unstructured marine food webs and "pollutant analogues." Fish. Bull., U.S. 70:1053-1059.

KEAST, A.
1970. Food specializations and bioenergetic interrelationships in the fish faunas of some small Ontario waterways. *In* J. H. Steele (editor), Marine food chains, p. 377-411. Univ. Calif. Press, Berkeley.
1978. Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. Environ. Biol. Fishes 3:7-31.

KEAST, A., AND D. WEBB.
1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23:1845-1874.

KISLALIOGLU, M., AND R. W. GIBSON.
1977. The feeding relationships of shallow water fishes in a Scottish sea loch. J. Fish Biol. 11:257-266.

LANGE, G. D., AND A. C. HURLEY.
1975. A theoretical treatment of unstructured food webs. Fish. Bull., U.S. 73:378-381.

LANGTON, R. W., AND R. E. BOWMAN.
1980. Food of fifteen Northwest Atlantic gadiform fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-740, 23 p.

LARKIN, P. A.
1978. Fisheries management—an essay for ecologists. Annu. Rev. Ecol. Syst. 9:52-73.

MILLS, E. L., AND R. O. FOURNIER.
1979. Fish production and the marine ecosystems of the Scotian Shelf, Eastern Canada. Mar. Biol. (Berl). 54:101-108.

NILSSON, N. A.
1967. Interactive segregation between fish species. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 295-313. Wiley, N.Y.

PALOHEIMO, J. E., AND L. M. DICKIE.
1970. Production and food supply. *In* J. H. Steele (editor), Marine food chains, p. 499-527. Univ. Calif. Press.

PIANKA, E. R.
1973. The structure of lizard communities. Annu. Rev. Ecol. Syst. 4:53-74.
1980. Guild structure in desert lizards. Oikos 35:194-201.
PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSON.
1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Fish Bull. 152, 105 p.
ROSS, S. T.
1977. Patterns of resource partitioning in sea robins (Pisces: Triglidae). Copeia 1977:561-571.
SCHOENER, T. W.
1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369-404.
1974. Resource partitioning in ecological communities. Science (Wash. D.C.) 185:27-39.
TYLER, A. V.
1971. Periodic and resident components in communities of Atlantic fishes. J. Fish. Res. Board Can. 28:935-946.
1972. Food resource division among northern, marine, demersal fishes. J. Fish. Res. Board Can. 29:997-1003.
VIRNSTEIN, R. W.
1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58:1199-1217.
WERNER, E. E.
1977. Species packing and niche complementarity in three sunfishes. Am. Nat. 111:553-578.
ZARET, T. M., AND A. S. RAND.
1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:336-342.

THE EFFECTS OF PHOTOPERIOD AND TEMPERATURE ON LABORATORY GROWTH OF JUVENILE *SEBASTES DIPLOPROA* AND A COMPARISON WITH GROWTH IN THE FIELD

Growth rates of fishes may act as sensitive indicators of environmental conditions. Variations in food supply, temperature, photoperiod, and other physical and biotic conditions may be reflected in the pattern of growth in a given species, yet the effect may vary depending upon the ontogenetic stage studied. Young stages, for example, generally tolerate and prefer higher temperatures than adults, both in the laboratory (Ferguson 1958; McCauley and Read 1973) and in the field (Brandt 1980); thermal optima for growth may similarly be higher. The present study examines the effects of temperature and photoperiod on growth rate in juveniles of the splitnose rockfish, *Sebastes diploproa*, in the laboratory and compares these growth rates with growth in the field. Adults of this species are benthic at depths of 200-500 m in the northeastern Pacific Ocean. *Sebastes* larvae are pelagic (Ahlstrom 1961), and prejuveniles of this species remain pelagic for about 1 yr, reaching maximum sizes near 55 mm standard length (SL) prior to migrating to the benthic habitat (Boehlert 1977). The thermal regime of the surface waters (13°-22° C) differs greatly from that in the adult habitat (6°-8° C; Reid et al. 1958), suggesting that temperature is an important factor in the life history of this species.

Materials and Methods

Prejuveniles were collected from under drifting kelp by dip net 8-18 km offshore from San Diego, Calif. (lat. 32°52′ N, long. 117°20′ W), and brought to the laboratory. Animals were initially maintained under ambient temperature and photoperiod, but these were changed at 0.5° C and 15 min/d, respectively, until reaching the two photoperiods and three temperatures of acclimation (12 light:12 dark, 16L:8D; 10°, 15°, and 20° C). Fish for the 12L:12D experiments were collected 17 March 1976 at 15.5° C; those for the 16L:8D experiments were collected 14 and 21 May 1976 at 17.7° and 17.6° C, respectively. When acclimation conditions were reached, standard lengths of all fish in each treatment were recorded. During the experiments fish were fed to satiation once daily on a mixture of Trout Chow,[1] ground squid, and frozen brine shrimp. An average of 26 fish were used for each experiment; the range of initial lengths was 30-55 mm SL.

Individual fish were not marked or tagged; individual growth rates were estimated by assuming that rank of individuals in length did not change during the experiment. This allowed determination of the size dependence of growth rate, subject to some unmeasured error if rank of individuals changed enough to affect estimated growth rate. These data were fit by photoperiod to quadratic response surface models using stepwise multiple regression (Nie et al. 1975) in the form

$$G = a + b_1 L_i + b_2 T + b_{11} L_i^2 + b_{22} T^2 + b_{12} L_i T$$

where G = growth rate (millimeters standard length per day), L_i = initial standard length (millimeters), T = temperature of acclimation (degrees Celsius), a = constant, and b_n = regression coefficients.

To compare the growth rates measured in the laboratory with growth of fish in the field, several specimens were collected for analysis of age using daily growth increments on the otoliths. Fish collected for age determination were taken to the laboratory alive where the otoliths were removed and stored dry in vials. Otoliths were processed for age determination as described in Taubert and Coble (1977). Briefly, otoliths (sagittae) were placed on slides with histological mounting medium and ground in sagittal sections. Small otoliths were ground on only one side whereas otoliths from fish >25 mm SL were removed from the slide, remounted, and ground on the other side. After the final grinding cover slips were placed over the otoliths. Each otolith was assigned a random number and read three times at least a week apart at 800 to 1,000 magnifications. If the range of three independent readings was not within 10% of the mean, the otolith readings were rejected.

Results

Mean laboratory growth rates were dependent upon temperature and photoperiod (Table 1). Comparison of mean daily growth rates, however, is confounded by the effects of initial length. At 16L:8D, growth rate was positively correlated with initial length at 10° C ($r = 0.78$) but negatively correlated at both 15° and 20° C ($r = -0.99$ in both cases, Figure 1A). At 12L:12D, growth rates were negatively correlated with initial length at 10° C ($r = -0.97$) and at 15° C ($r = -0.94$) but positively correlated with initial length at 20° C ($r = 0.42$, Figure 1B). In the latter experiment, however, the length range was not as complete as in the other experiments (Table 1).

The relationship of growth to temperature and initial length are more easily interpreted with the multiple regression models. Regression coefficients for the growth response models were all significant with the exception of the length squared term (Table 2). Effects of temperature were similar at both photoperiods; growth increased to some optimum temperature and then declined (Figure 2A, B), as indicated by the negative value of the regression coefficient for temperature squared, b_{22} (Table 2). The apparent temperatures of optimum growth increased slightly with length at 12L:12D but decreased with length at 16L:8D (Figure 2A, B). Initial length showed a clear relationship with growth at 12L:12D (Figure 2B). At all temperatures, growth decreased with increasing length; zero growth, observed in the 10° C experiment at the largest sizes (Table 1), is predicted by the model at sizes >50 mm SL within the range of temperatures studied. At 16L:8D, the growth response to initial length is more complex. At approximately 10.5° C the model predicts a

TABLE 1.—Length-frequency distributions at the start and end of the growth experiments for laboratory acclimated prejuvenile *Sebastes diploproa* at two photoperiods and three temperatures. N = number of fish in the experiment, $\bar{X}$ = mean standard length (millimeters), Δ = change in the sum of lengths (millimeters) between start and end of each experiment, t = duration of the experiment in days.

	12L:12D						16L:8D					
	10°		15°		20°		10°		15°		20°	
SL (mm)	Start	End	Start	End	Start	End	Start	End	Start	End	Start	End
30	1		4		2		1		2			
31	2		3		1		1		1		1	
32	2		4		2						1	
33	4		5		3							
34	4		4		2						3	
35	4		4	1	6	1	3		3			
36	3		2		3	2		1	1			
37					3	2						
38	3				4	4		1				
39	2	3		1	1	3						
40	3	3		2		6						3
41	1	7	2		1	2		2	1			
42	2	4		7		2	1		1			1
43	1	6		4		2	1	1				1
44	1	3	1	5		1	3					
45				5		2	1			1		
46		6	1	1			4		2	1	3	
47				2		1	2			2	2	
48			1	1			1		2		4	
49		1		1			1	1	2	1	1	
50	1						1	2	2	2	2	2
51	2	3		1					2			3
52			1					2	1		2	3
53								1		1		3
54	1			1				2			1	1
55	1	2						2		1		2
56								1		2		1
57								2		1		
58								1		3		
59										2		
60								1		3		
N	38	38	32	32	28	28	20	20	20	20	20	20
$\bar{X}$	38.3	43.9	35.2	44.0	35.1	40.1	42.7	50.6	42.8	54.2	44.8	49.7
Δ	213		281		140		158		228		97	
t	54		54		53		53		54		51	
Growth (mm/d)	.105		.164		.093		.150		.211		.096	

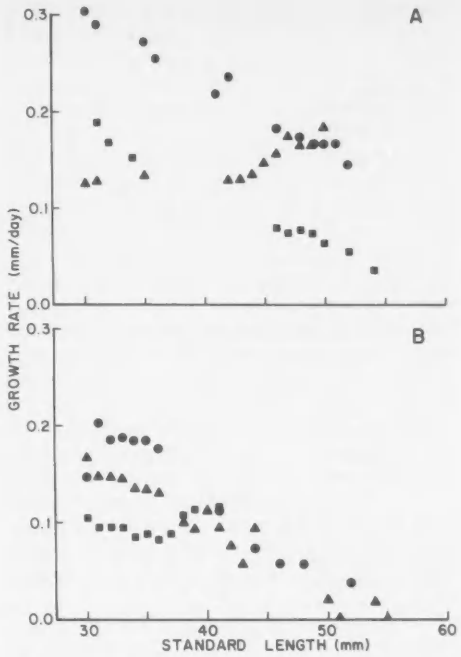

FIGURE 1.—Relationship of initial fish length with measured growth rates during A) 16L:8D experiments, B) 12L:12D experiments. Triangles represent values for fish acclimated to 10° C; dots, 15° C; squares, 20° C.

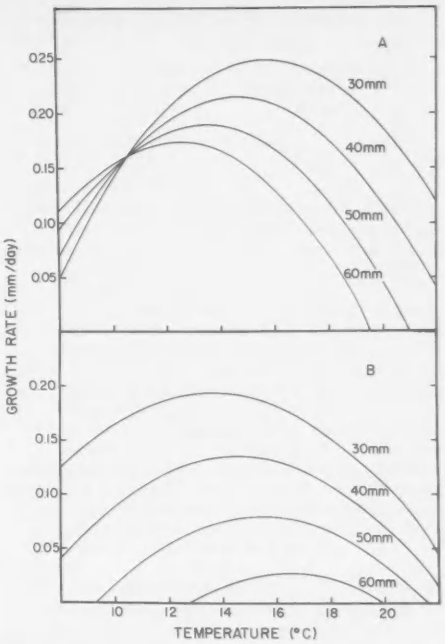

FIGURE 2.—Growth response surfaces for given isopleths of initial standard length as predicted by the multiple regression models. A) 16L:8D experiments, B) 12L:12D experiments.

nodal point where fish of all initial lengths are characterized by the same growth rate (Figure 2A). Below that temperature, growth increases with increasing length, whereas at higher temperatures, it decreases with increasing length. The response of growth to photoperiod indicates a generally positive relationship (Figure 2A, B), with faster growth under most conditions at 16L:8D. Growth with length at all temperatures at 12L:12D and at higher temperatures at 16L:8D decreases with length, suggesting a temperature-dependent asymptote for growth. For low temperatures at 16L:8D, however, growth increases with length and no asymptote is apparent.

TABLE 2.—Coefficients and related statistics for the growth response models for laboratory growth in *Sebastes diploproa*. Multiple correlation coefficients (R) were 0.919 and 0.933 for 12L:12D and 16L:8D, respectively.

	12L:12D (N = 98)			16L:8D (N = 60)		
Item	Value	SE	P	Value	SE	P
a	0.1378	0.0729	0.062	−0.8090	0.0919	0.001
b_1	−.0112	.0016	.001	.0080	.0018	.001
b_2	.0459	.0073	.001	.1264	.0087	.001
b_{22}	−.0021	.0002	.001	−.0033	.0003	.001
b_{12}	.0004	.0001	.003	−.0007	.0001	.001

Growth of fish collected in the field was determined from daily growth increments. Otoliths from 53 specimens were processed as described. Due to broken or unclear otoliths, loss of material from the margin during grinding, or failure to meet the criterion of consistency in age from the three readings, 21 ages were determined. These 21 fish were collected in April (6), August (2), September (3), October (1), and December (9) from 1973 through 1978. Thus a variety of surface temperatures and thermal histories were experienced by these fish. Fish ranged from 9.0 to 42.7 mm SL; the age ranged from 43 to 205 d. The resultant pattern of growth in the field was linear over the size range studied (Figure 3). The growth rates for these specimens, averaged over the

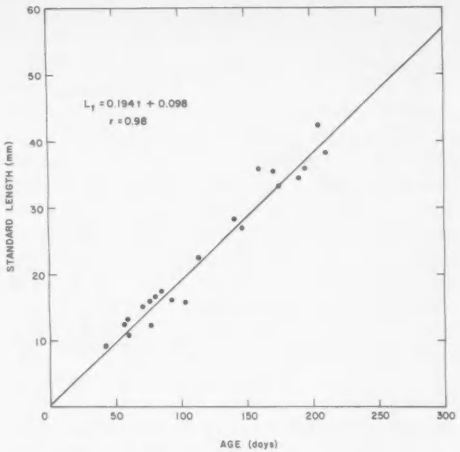

FIGURE 3.—Age at length for field-captured prejuvenile *Sebastes diploproa* as determined by analysis of daily growth increments on otoliths. L_t = length at time t (days).

lifetime of each fish, ranged from 0.154 to 0.225 mm SL/d, with the mean value indicated by the slope of the line, 0.194 mm SL/d. These rates were similar to predicted laboratory growth rates under a variety of temperature and initial length conditions at 16L:8D (Figure 2A) but only to the smallest fish between 10° and 18° C at 12L:12D (Figure 2B). *Sebastes diploproa* apparently grows more slowly in the field than pelagic juvenile *S. melanostomus* of similar size, the only other species of *Sebastes* whose growth has been estimated using daily growth increments (Moser and Ahlstrom 1978).

Discussion

Fish growth generally reaches a maximum at some optimum temperature and decreases at temperatures above and below this level (Brown 1957; Brett 1979), approaching zero near lethal temperatures. Upper lethal temperatures (critical thermal maxima) for prejuvenile *S. diploproa* range from 26° to 30° C, depending upon the temperature of acclimation (Boehlert 1981), and prejuveniles tolerate surface temperatures up to 23° C. The optimum temperature for growth of juvenile *S. diploproa* depends upon both photoperiod and fish length. The growth models suggest optimum temperatures for growth which increase with length at 12L:12D from 13.8° C at 30 mm SL to 15.7° C at 50 mm SL (Figure 2B) and decrease with length at 16L:8D from 16.0° C at 30 mm to 13.8° C at 50 mm SL (Figure 2A). These temperatures clearly exceed those experienced by later benthic juveniles and adults.

Longer photoperiod enhanced growth at nearly all conditions of fish length and temperature (Table 1; Figures 1, 2). Increased growth with longer photoperiod has been observed in green sunfish (Gross et al. 1965), plaice and sole (Fonds 1979), and Baltic salmon parr (Lundqvist 1980). Brown (1946b), however, observed lower growth rate of brown trout in long photoperiods. As the fish in the present experiments were fed to satiation only once daily, it is reasonable to assume that rations under both photoperiods were similar. Surface prejuvenile *S. diploproa* acclimated to short photoperiods have greater standard metabolic rates than those acclimated to long photoperiods at the same acclimation temperatures (Boehlert 1978). Thus the enhanced growth in the longer photoperiod may be related to a greater scope for growth (Elliot 1976) due to lower standard metabolic rates.

The dependence of growth on fish size in the present study is interesting in relation to the life history of this species. Other investigators have observed both increases and decreases in the size range of fishes at the beginning and end of growth experiments. Brown (1946a) described the "size hierarchy effect," which apparently results from development of a peck order with larger fish dominant (Stringer and Hoar 1955). No dominance or peck order with respect to feeding was apparent in the experiments with *S. diploproa*, and in four of six experiments, growth rate decreased with increasing size (Figure 1), as is predicted by the growth models (Figure 2). Laboratory and field growth rates were similar for fish at approximately the same lengths, but it is uncertain whether the decreased growth apparent with increasing length observed in the laboratory occurs in the field. The largest specimen from the field successfully aged using daily growth increments on the otoliths was 42.7 mm SL, below the size at which significantly decreased growth rates occured in the laboratory (Figure 1). If an asymptote does exist in the field, it fits well with the largest pelagic prejuvenile captured in the field (59 mm SL; Boehlert 1977) and with the maximum size after growth in the present study (60 mm SL, Table 1).

The parturition season for *S. diploproa* off California is February through July (Phillips 1964), with possible limited year-round spawning (Boehlert 1977). This results in poorly defined year classes and length-frequency distributions, yet a size threshold and distinct season exist for migration from the surface to the benthic habitat (Boehlert 1977, 1978). Zamakhaev (1964) suggested that size discrepancy within an age-group may be minimized through compensatory growth. The observed pattern of reduced growth at sizes >40 mm SL may serve as a variant on the phenomenon of compensatory growth, consolidating the 0-group fish at sizes near 50 mm SL prior to the migration, which occurs from May through September (Boehlert 1978). At the onset of migration, the oldest and largest fish would migrate first, as observed in sockeye salmon (Foerster 1937) and Atlantic salmon (Elson 1957). Smaller fish would continue rapid growth, and as they reached the size threshold, would also migrate.

Initiation of the surface-to-benthic migration of juvenile *S. diploproa* may be dependent upon photoperiod or rate of change of photoperiod subject to an endogenous program which depends upon a size threshold (Boehlert 1978, 1981). The temperature change between surface and benthic habitats is about 12° C, suggesting that temperature is an important consideration in the migration. Although there is no change in critical thermal maximum for juvenile *S. diploproa* acclimated to the same temperature but different photoperiods (Boehlert 1981), prejuveniles from the field are metabolically preadapted for the lower temperatures during the migratory season (Boehlert 1978). The size dependence of growth in the present experiments suggests a downward shift in the temperature of optimum growth with increasing size in 16L:8D but not in 12L:12D. Photoperiod may thus interact with size, resulting in an ontogenetic change in thermal requirements.

Acknowledgments

The laboratory growth experiments were conducted at the Southwest Fisheries Center, La Jolla, Calif., and were partially supported by the Institute of Marine Resources and by the Hubbs-Sea World Research Institute. Analysis of daily growth increments was conducted while the author held a National Research Council Postdoctoral Associateship at the Northwest and Alaska Fisheries Center, Seattle, Wash. I thank an anonymous reviewer for valuable suggestions on the manuscript.

Literature Cited

AHLSTROM, E. H.
1961. Distribution and relative abundance of rockfish (*Sebastodes* spp.) larvae off California and Baja California. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 150:169-176.

BOEHLERT, G. W.
1977. Timing of the surface-to-benthic migration in juvenile rockfish, *Sebastes diploproa*, off southern California. Fish. Bull., U.S. 75:887-890.
1978. Changes in the oxygen consumption of prejuvenile rockfish, *Sebastes diploproa*, prior to migration from the surface to deep water. Physiol. Zool. 51:56-67.
1981. The role of temperature and photoperiod in the ontogenetic migration of prejuvenile *Sebastes diploproa* (Pisces: Scorpaenidae). Calif. Fish Game 67:164-175.

BRANDT, S. B.
1980. Spatial segregation of adult and young-of-the-year alewives across a thermocline in Lake Michigan. Trans. Am. Fish. Soc. 109:469-478.

BRETT, J. R.
1979. Environmental factors and growth. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology, Vol. VIII, p. 599-675. Acad. Press, N.Y.

BROWN, M. E.
1946a. The growth of brown trout (*Salmo trutta* Linn.). I. Factors influencing the growth of trout fry. J. Exp. Biol. 22:118-129.
1946b. The growth of brown trout (*Salmo trutta* Linn.). II. The growth of two-year-old trout at a constant temperature of 11.5° C. J. Exp. Biol. 22:130-144.
1957. Experimental studies on growth. *In* M. E. Brown (editor), The physiology of fishes, Vol. I, p. 361-400. Acad. Press, N.Y.

ELLIOT, J. M.
1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. J. Anim. Ecol. 45:923-948.

ELSON, P. F.
1957. The importance of size in the change from parr to smolt in Atlantic salmon. Can. Fish. Cult. 21:1-6.

FERGUSON, R. G.
1958. The preferred temperatures of fish and their midsummer distribution in temperate lakes and streams. J. Fish. Res. Board Can. 15:607-624.

FOERSTER, R. E.
1937. The relation of temperature to the seaward migration of young sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 3:421-438.

FONDS, M.
1979. A seasonal fluctuation in growth rate of young plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the laboratory at constant temperatures and a natural daylight cycle. *In* E. Naylor and R. G. Hartnoll (editors), Cyclic phenomena in marine plants and animals, p. 151-156. Pergamon Press, N.Y.

GROSS, W. L., E. W. ROELOFS, AND P. O. FROMM.
1965. Influence of photoperiod on growth of green sunfish, *Lepomis cyanellus*. J. Fish. Res. Board Can. 22:1379-1386.
LUNDQVIST, H.
1980. Influence of photoperiod on growth in Baltic salmon parr (*Salmo salar* L.) with special reference to the effect of precocious sexual maturation. Can. J. Zool. 58:940-944.
MCCAULEY, R. W., AND L. A. A. READ.
1973. Temperature selection by juvenile and adult yellow perch (*Perca flavescens*) acclimated to 24°C. J. Fish. Res. Board Can. 30:1253-1255.
MOSER, H. G., AND E. H. AHLSTROM.
1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Board Can. 35:981-996.
NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT.
1975. Statistical package for the social sciences. 2d ed. McGraw Hill, N.Y., 675 p.
PHILLIPS, J. B.
1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.
REID, J. L., JR., G. I. RODEN, AND J. G. WYLLIE.
1958. Studies of the California Current system. Calif. Coop. Oceanic Fish. Invest. Prog. Rep. 1 July 1956 to 1 Jan. 1958. p. 27-57.
STRINGER, G. E., AND W. S. HOAR.
1955. Aggressive behavior of underyearling Kamloops trout. Can. J. Zool. 33:148-160.
TAUBERT, B. D., AND D. W. COBLE.
1977. Daily rings in otoliths of three species of *Lepomis* and *Tilapia mossambica*. J. Fish. Res. Board Can. 34:332-340.
ZAMAKHAEV, D. F.
1964. On the influence of the growth in the first years of life on further growth in fish. [In Russ., Engl. summ.] Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO), Tr. Vses. Nauchno-Issled. 50:109-141. (Fish. Res. Board Can., Transl. Ser. 549, 39 p.)

GEORGE W. BOEHLERT

School of Oceanography, Oregon State University
Marine Science Center
Newport, OR 97365

A CORRELATION BETWEEN ANNUAL CATCHES OF DUNGENESS CRAB, *CANCER MAGISTER*, ALONG THE WEST COAST OF NORTH AMERICA AND MEAN ANNUAL SUNSPOT NUMBER

A recent paper by Driver (1978) described the prediction of shrimp landings off northwest England based on sunspot activity. Stimulated by this work, we examined the relationship between the Dungeness crab, *Cancer magister*, commercial fishery off the west coast of North America and mean annual sunspot number. The Dungeness crab is commercially important and its fluctuating catch has made it the subject of numerous papers (Reed 1969; Peterson 1973; Botsford and Wickham 1975, 1978), some of which noted a distinct rhythm in annual catch. Moreover, Dungeness crab catch statistics are particularly favorable for this study, as it has been estimated that almost every legal crab within the species' range is taken during the commercial season (Pacific Marine Fisheries Commission 1965) and hence there was no need to factor fishing effort into the computations.

Catch statistics were provided by the Pacific Marine Fisheries Commission and comprise commercial landings made in Alaska, British Columbia, Washington, Oregon, and California from 1955 (the earliest year for which complete records were available) to 1980. We utilized the mean annual sunspot values in Waldmeier (1961, 1978) with additional data supplied by Adkins[1] and Eddy.[2] Data were plotted (Figure 1) and correlation coefficients and associated values generated by linear regression (Table 1) for two complete cycles, 1955-64 and 1965-75.

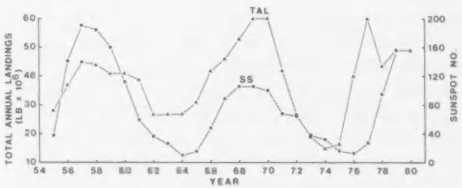

FIGURE 1.—Total annual landings of Dungeness crabs off the west coast of North America (TAL) and mean annual sunspot number (SS) for the period 1955 through 1980.

TABLE 1.—The correlation between commercial Dungeness crab catch and mean annual sunspot number off the west coast of North America.

Period	*r*	df	*f*-ratio	*P*
1955-64	0.90	1, 8	35.3	<0.001
1965-75	.87	1, 9	29.3	<.001

Dungeness crab catches and sunspot numbers both varied in approximately 11-yr cycles and the cycle periods for the two were strongly correlated

[1]J. Adkins, Solar Observer, Mt. Wilson and Las Canpanis Observatory, 813 Santa Barbara Street, Pasadena, Calif., pers. commun. August 1980.
[2]J. Eddy, High Altitude Observatory, National Center for Atmospheric Research, Boulder, CO 80307, pers. commun. March 1981.

(1955-64, r = 0.90; 1965-75, r = 0.87) as the peak catches of 1957, 1969, and 1970 closely corresponded to sunspot maxima years 1957, 1968, and 1969. However, the amplitude of the two phenomena appeared to be asynchronous. The very high sunspot peak of 1957 saw a considerably lower peak crab catch than did the relatively low sunspot peak of 1969.

Woelke[3] suggested that Dungeness crab landings were influenced by water temperature during the crabs' larval stage about 4 yr before, with temperatures at that time being inversely correlated to landings. We analyzed the relationships between crab catches and the sunspot numbers of 4 and 5 yr previous. Correlation coefficients were generated for two crab catch cycles (cycle 1 = 1955-64; cycle 2 = 1965-74). The highest correlation (cycle 1, r = 0.82; cycle 2, r = 0.95) was between Dungeness crab catches and the sunspot number of 5 yr before (Figure 2, Table 2). The correlation was strongly negative. That is, high sunspot number in a particular year seemed to be a predictor of relatively low crab catches 5 yr hence.

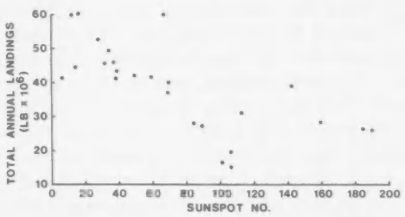

FIGURE 2.—Mean annual sunspot numbers (SS) of the years 1950-69 plotted against total annual landings of Dungeness crabs (TAL) 5 yr later (1955-74).

TABLE 2.—The correlation between commercial Dungeness crab catches and the mean annual sunspot number 5 yr previous (cycle 1 = sunspots of 1950-59, crab landings 1955-64; cycle 2 = sunspots of 1960-69, crab landings 1965-74).

Period	r	df	f-ratio	P
Cycle 1	0.82	1, 8	16.7	<0.01
Cycle 2	.95	1, 9	87.6	<.001
Cycles 1 and 2	.89	1, 23	20.8	<.01

A number of factors may be involved in the cyclical *C. magister* catches. Upwelling, by influencing food density, may have an effect (Peterson 1973). Water temperature and salinity, as well as current pattern may influence larval survival (Lough 1976). Botsford and Wickham (1975) felt that density-dependent biotic factors, such as cannibalism, might play a part.

However, as Eddy (1979) stated, in discussing sunspot studies, "We start into the deep waters of uncertainty not from rocks but from the sand, and with statistics our only lifeline." Sunspots, relatively dark areas about 2000°K cooler than their surroundings, have been noted for more than 1,500 yr (Herman and Goldberg 1978). In the past 200 yr, sunspot activity has been correlated to many planetary processes. Statistical correlations have been made between sunspots and both climatological and biological phenomena (Gnevyshev and Ol' 1977; Pittock 1978). However, increased sunspot activity brings about only slight changes in both magnetic fields and incident radiation levels and, unfortunately, there exists no completely acceptable hypothesis which explains how these slight alterations act on the various processes.

Thus, whether sunspot activity somehow influences any of the above (including crab catches) is unknown. The work of Southward et al. (1975) suggests that an array of events, including intertidal barnacle, *Chthalamus* sp., numbers, hake and cod trawl catches and pilchard egg densities are correlated, in 11-yr cycles, to sunspot number. There is the strong suggestion in this work that sea surface temperature (also strongly correlated to sunspot activity) may be responsible for the cyclical events. Hence, sunspot activity may be linked to biotic events through the agencies of another level of phenomena (in this case temperature).

Whether the crab catch and sunspot cycles remain congruent will have to be seen. Other correlations of this nature have proven spurious with time. If the pattern holds, however, annual sunspot number may be a useful predictor of Dungeness crab catch, delineating periods of catch maxima and minima and perhaps predicting catch amplitude, i.e., how many crabs will be taken.

Acknowledgments

We would like to thank J. Eddy and P. Gilman for enlightening discussions on solar activity, S. Penn and K. Zerba for the illustrations, and S. Warschaw and J. Schulz for typing the manuscript.

[3]Woelke, C. E. 1971. Some relationships between temperature and Pacific Northwest shellfish. Proc. 51st Annu. Conf., Western Assoc. Game Fish Comm., p. 132-135.

Literature Cited

BOTSFORD, L. W., AND D. E. WICKHAM.
1975. Correlation of upwelling index and Dungeness crab catch. Fish Bull., U.S. 73:901-907.
1978. Behavior of age-specific, density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. 35:833-843.

DRIVER, P. A.
1978. The prediction of shrimp landings from sunspot activity. Mar. Biol. (Berl.) 47:359-361.

EDDY, J. A.
1979. Book review—Effects of solar activity on the earth's atmosphere and biosphere. Icarus 37:476-477.

GNEVYSHEV, M. N., AND A. I. OL' (editors).
1977. Effects of solar activity on the earth's atmosphere and biosphere. Keter Press, Jerus., 290 p.

HERMAN, J. R., AND R. A. GOLDBERG.
1978. Sun, weather and climate. NASA (Natl. Aeronaut. Space Adm.) Sci. Publ. 426, 360 p.

PACIFIC MARINE FISHERIES COMMISSION.
1965. Discussion following the report on Dungeness crabs. 16th and 17th Annu. Rep. Pac. Mar. Fish. Comm., p. 38-39.

PETERSON, W. T.
1973. Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the west coast of the United States. Fish. Bull., U.S. 71:902-910.

PITTOCK, A. B.
1978. A critical look at long-term sun-weather relationships. Rev. Geophys. Space Phys. 16:400-420.

REED, P. H.
1969. Culture methods and effects of temperature and salinity on survival and growth of Dungeness crab (*Cancer magister*) larvae in the laboratory. J. Fish. Res. Board Can. 26:389-397.

SOUTHWARD, A. J., E. I. BUTLER, AND L. PENNYCUICK.
1975. Recent cyclic changes in climate and in abundance of marine life. Nature (Lond.) 253:714-717.

WALDMEIER, M.
1961. The sunspot-activity in the years 1610-1960. Schulthess, Zur. Switz., 171 p.
1978. Solar activity 1964-1976 (cycle no. 20). Astronom. Mitt. Eidg. sternwarte Zur. 368, 33 p.

MILTON S. LOVE
WILLIAM V. WESTPHAL

Department of Biology, Occidental College
1600 Campus Road
Los Angeles, CA 90041

FECUNDITY OF THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*, IN NEWFOUNDLAND WATERS

In lobster (genus *Homarus*) fisheries generally, current minimum legal size limits are below the size at 50% female maturity and fishing mortality rates are very high (Anonymous 1979). Under such conditions, widespread recruitment overfishing appears to be a distinct possibility. Conventional yield per recruit assessment models are not totally adequate when dealing with lobsters and this has led to the development of models which are much more species oriented (Caddy 1977, 1979; Ennis and Akenhead 1978). A feature of these models which resulted from concern with recruitment overfishing is provision for assessing the effect on population fecundity of changes in size limit and fishing mortality. In addition to size-maturity information, such assessments require data on fecundity.

Unfortunately, the general applicability of size-fecundity relationships for the American lobster, *Homarus americanus*, which are available from the literature, is suspect. Saila et al. (1969) concluded that the methodology used by Herrick (1911) resulted in quite substantial overestimates of egg numbers. The size-fecundity relationship Saila et al. (1969) presented was based on samples obtained from three widely separated areas; however, Squires (1970) and Squires et al. (1974) suggested that size-fecundity relationships for American lobsters in different areas could be quite different. Squires' (1970) methodology was similar to that of Herrick but he found that his estimates varied from actual counts by $<2\%$, an error factor comparable with that reported by Saila et al. (1969) and Perkins (1971) using electronic counters. Aiken and Waddy (1980) suggested that standardized egg counts from different areas would clarify the question of geographic variation in American lobster fecundity and concluded that Herrick's estimates should not be dismissed until the results of these or other, more explicit studies are available.

This paper presents new fecundity data for a Newfoundland area as a contribution to the literature on the subject and provides comparisons with published size-fecundity relationships.

Materials and Methods

Ovigerous females were included in samples ob-

tained during spring (near the end of the incubation period) trap fishing in the area of Arnold's Cove, Placentia Bay, on the southeast coast of Newfoundland in 1969, and in the areas of Ship Harbour and Paradise in Placentia Bay in 1970 (Figure 1). Portions of the samples (up to 50 American lobsters) were usually held in floating wooden boxes (about 100-lb capacity) for several days before being subjected to detailed biological examination. Carapace lengths (millimeters) were recorded and the abdomens of ovigerous specimens with attached egg masses were preserved individually in 10% Formalin.[1] Loss of eggs over the holding period cannot be discounted, but it is felt that such losses were minimal.

Eggs were removed from the pleopods, washed on a screen of fine-meshed plankton netting to remove the larger pieces of connective tissue and other material, and then left to soak in freshwater overnight. After soaking, the eggs were spread thinly over very shallow pans to dry at room temperature until they were quite hard (usually after about 24 h) and could withstand being rubbed over a fine-meshed screen to remove the remaining connective tissue. After drying and final cleaning, the weight of the egg sample was obtained (to the nearest 0.0001 g). A subsample, representing approximately 1/30 of the whole sample (as determined by weighing), was weighed and the eggs counted manually. The number of eggs in the whole sample was then calculated.

To determine the error associated with this method, total numbers for 11 samples were determined by actual counts for comparison with the estimated total numbers for the same samples. The error ranged from −3.6% to 0.04% and for the 11 sets of counts totaled the error was 0.54%.

Carapace length and fecundity data were log (base 10) transformed and the linearized version of the power curve was fitted to each set. The linear relationships thus derived were compared by analysis of covariance.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

FIGURE 1.—Map of Newfoundland showing places mentioned in the text.

Results and Discussion

Curvilinear size-fecundity relationships derived from log-log (base 10) regression analysis for spring-caught (April-June) samples are presented for three areas in Placentia Bay, along with the same relationships obtained from reanalysis of the data presented by Squires (1970) and Squires et al. (1974) for two Newfoundland west coast areas (Figure 2, Table 1). The methodology of Squires (1970) and Squires et al. (1974) was similar to that used here except that the estimates were determined volumetrically instead of by weighing. These estimates varied from actual counts by $<2\%$ which is within the range of error determined in this study. For this reason the following statistical comparisons between the Placentia Bay and west coast samples are considered valid.

An F_{MAX} test on the log-transformed data demonstrated significantly different ($P<0.01$) residual variances among the five samples. Various combinations of the log-log relationships were compared by analysis of covariance. In all comparisons between relationships for Placentia Bay and the comparison between the two relationships for the west coast, residual variances were similar. However, in all comparisons between one of the Placentia Bay and one of the west coast relationships, residual variances were significantly different (Table 2). Two of the four sets of relationships with similar residual variances had significantly different slopes, the other two had similar slopes but significantly different means. There was wide variation in fecundity at size and the samples differed in size composition (Table 3). Significant differences in these relationships may result in large part from differences in sample size and size composition.

Samples with at least six specimens in the same 5 mm size group were compared by analysis of variance. There is some size-related variation in fecundity within each 5 mm size group. This could confound a comparison if, in the samples being compared, there is clustering of specimens at opposite ends of the size range. Upon examination it was found that for each sample compared in Table 4 the specimens were fairly well distributed throughout the 5 mm size range and it is assumed that size-related variation does not invalidate

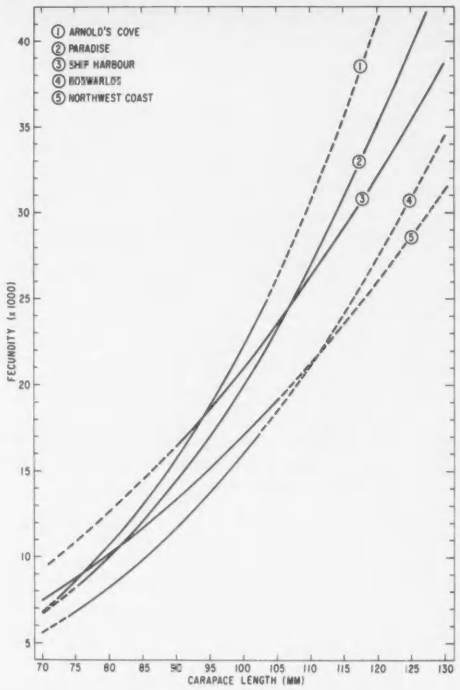

FIGURE 2.—Carapace length-fecundity relationships for American lobsters from three areas in Placentia Bay, Newfoundland and two areas on the west coast of Newfoundland. Dashed lines indicate extrapolations beyond the data.

TABLE 1.—Regression equations from which the curvilinear relationships shown in Figure 1 were derived.

Sample	*N*	Carapace length range (mm)	Regression equation	*r*
Arnold's Cove	43	72-104	$\log_{10} F = 3.3471 \log_{10} CL - 2.3437$	0.88
Paradise	72	75-139	$\log_{10} F = 3.0984 \log_{10} CL - 1.8963$	.94
Ship Harbour	68	89-159	$\log_{10} F = 2.3188 \log_{10} CL - 0.3117$	.89
Boswarlos	75	74-103	$\log_{10} F = 2.9387 \log_{10} CL - 1.6747$	.58
Northwest coast	63	70-107	$\log_{10} F = 2.3161 \log_{10} CL - 0.3998$	.60

TABLE 2.—Results of analyses of covariance of size-fecundity relationships presented in Figure 1.

	Mean squares		Slopes		Means	
Relationships compared	*F*	*P*	*F*	*P*	*F*	*P*
Arnold's Cove vs. Ship Hr.	1.29	>0.20	9.44	<0.01		
Arnold's Cove vs. Paradise	1.27	>.20	.57	.542	6.29	0.013
Paradise vs. Ship Hr.	1.02	>.50	15.86	<.001		
Arnold's Cove vs. Boswarlos	3.08	<.001				
Arnold's Cove vs. NW coast	3.48	<.001				
Boswarlos vs. NW coast	1.13	>.50	.98	.674	15.08	<.0001
Paradise vs. Boswarlos	2.42	<.001				
Paradise vs. NW coast	2.73	<.001				
Ship Hr. vs. NW coast	2.69	<.001				
Ship Hr. vs. Boswarlos	2.38	<.001				

TABLE 3.—Summary of fecundity data on which relationships shown in Figure 1 are based.

Carapace length	Arnold's Cove			Paradise			Ship Harbour			Boswarlos			Northwest coast		
	N	$\bar{X}$	Range	*N*	$\bar{X}$	Range	*N*	$\bar{X}$	Range	*N*	$\bar{X}$	Range	*N*	$\bar{X}$	Range
66- 70													1	4,700	
71- 75	3	9,096	8,293-10,115	1	6,756					4	8,000	7,000- 9,300	4	10,075	9,100-11,500
76- 80	4	9,375	7,299-11,423	12	9,716	7,727-12,535				37	8,178	4,600-11,800	14	10,236	6,800-15,100
81- 85	12	11,821	9,894-13,479	16	11,391	7,112-15,704				21	8,414	3,500-12,800	21	11,214	6,700-16,100
86- 90	11	14,393	9,836-19,909	9	13,156	10,245-16,992	1	13,773		8	10,850	7,800-15,300	8	13,887	9,400-18,800
91- 95	8	18,085	15,833-20,858	8	16,445	11,248-20,767	6	17,348	12,703-22,555	3	13,667	13,000-14,000	7	13,500	6,900-22,100
96-100	3	21,432	16,414-29,888	8	19,697	14,304-24,421	4	20,291	12,926-24,875	1	19,200		5	20,240	16,700-23,900
101-105	2	23,379	22,535-24,223	4	26,213	24,477-27,530	4	22,544	21,351-25,216	1	22,800		2	12,500	10,700-14,300
106-110				3	24,920	20,477-30,099	5	26,266	22,548-28,878				1	26,000	
111-115				3	29,462	25,516-33,660	6	32,559	27,894-36,896						
116-120				2	38,536	34,621-42,450	12	32,247	24,135-43,116						
121-125				2	39,778	32,887-46,669	6	32,018	19,915-38,601						
126-130				1	36,337		4	40,794	34,078-45,443						
131-135				2	42,591	41,645-43,537	6	43,467	37,882-49,681						
136-140				1	42,837		5	46,038	40,638-55,937						
141-145							4	44,511	36,395-57,457						
146-150							2	47,904	47,716-48,092						
151-155							2	56,986	52,399-61,573						
156-160							1	56,995							

these comparisons. All comparisons between Placentia Bay samples showed no significant differences (Table 4). For the comparisons between the two west coast samples and between samples from each of the two areas, there were significant differences for some size groups but not for others. The relationships shown in Figure 2 indicate that American lobsters in Placentia Bay are more fecund than those on the west coast. This observation is supported by the analysis of covariance and to a lesser extent by the analysis of variance.

Data for the three Placentia Bay areas were combined as were data for the two west coast areas. The curvilinear relationships derived from log-log regression analysis were plotted with those available from the literature for other areas (Figure 3). Substantial differences in size-fecundity relationships between some of these areas are apparent.

Perkins (1971) reported substantial egg loss during incubation (36% between October and June) for American lobsters from the offshore canyon areas of the northeast United States. This should not be a significant factor in the above comparisons, however, since in all cases samples were ob-

TABLE 4.—Results of analyses of variance of fecundity data for different size groups from the various samples.

Samples compared	Size groups (mm)			
	76-80	81-85	86-90	91-95
Arnold's Cove vs. Paradise	—	NSD	NSD	NSD
Arnold's Cove vs. Ship Hr.	—	—	—	NSD
Paradise vs. Ship Hr.	—	—	—	NSD
Arnold's Cove vs. Boswarlos	—	**	*	—
Arnold's Cove vs. NW coast	—	NSD	NSD	NSD
Paradise vs. Boswarlos	*	**	NSD	—
Paradise vs. NW coast	NSD	NSD	NSD	NSD
Ship Hr. vs NW coast	—	—	—	NSD
Boswarlos vs. NW coast	**	**	NSD	—

NSD = no significant difference $P \geq 0.05$, $*0.01 < P < 0.05$, $**P < 0.01$.

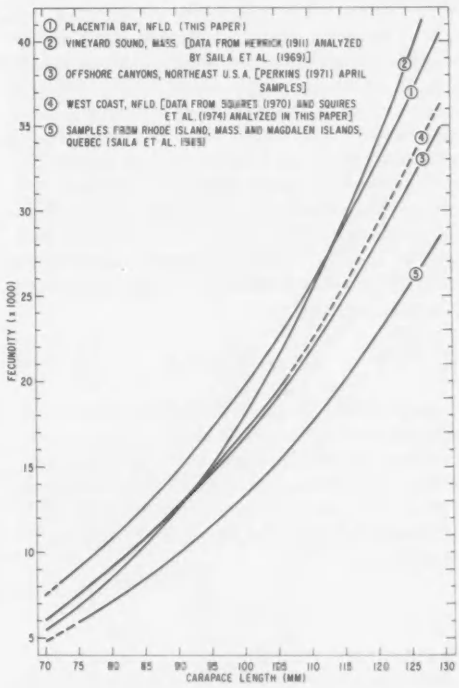
① PLACENTIA BAY, NFLD. (THIS PAPER)
② VINEYARD SOUND, MASS. [DATA FROM HERRICK (1911) ANALYZED BY SAILA ET AL. (1969)]
③ OFFSHORE CANYONS, NORTHEAST U.S.A. [PERKINS (1971) APRIL SAMPLES]
④ WEST COAST, NFLD. [DATA FROM SQUIRES (1970) AND SQUIRES ET AL. (1974) ANALYZED IN THIS PAPER]
⑤ SAMPLES FROM RHODE ISLAND, MASS. AND MAGDALEN ISLANDS, QUEBEC (SAILA ET AL. 1969)
FECUNDITY (x 1000)
CARAPACE LENGTH (MM)

FIGURE 3.—Carapace length-fecundity relationships for American lobsters from two Newfoundland areas and those available for the literature for other areas. Dashed lines indicate extrapolations beyond the data.

tained dur ng late spring-early summer towards the end of the incubation period.

Fecundity values calculated from the relationships in Figure 2 range from 4,800 to 7,450 at 70 mm carapace length and from 25,400 to 38,300 at 125 mm. The relationship of Saila et al. (1969) gives the lowest values over the entire range of sizes considered. This relationship is suspect, however, since it is based on samples obtained from three widely separated areas. Over most of the size range considered the relationship for Placentia Bay gives higher estimates than those from the relationship derived by Saila et al. (1969) from Herrick's (1911) data, indicating that Herrick's data should not be discounted as Saila et al. (1969) suggested.

Definitive statistical comparisons of size-fecundity relationships for American lobsters from different areas would require large samples which adequately cover a wide range of sizes. Even with such samples comparisons could be somewhat confounded by geographic variation in size at first maturity, which, for certain areas, would preclude direct comparison of fecundity at smaller sizes. In addition, samples would have to be taken at approximately the same stage in the incubation period by the same method of capture and be subjected to similar handling and procedures for determining egg numbers. These requirements are unlikely to be met in the foreseeable future. However, as tenuous as the comparisons presented here may be, they do suggest substantial geographic variation in size-fecundity relationships for American lobsters.

Acknowledgments

I am grateful to G. Dawe who participated in the collection of samples and, with the assistance of a number of casual employees, carried out the tedious task of obtaining egg counts. The assistance of P. W. Collins in performing the various data analyses and drafting the figures is also gratefully acknowledged.

Literature Cited

ANONYMOUS.
1979. Report of the *Homarus* Working Group. ICES (Int. Counc. Explor. Sea) C.M. 1979/K:8, 49 p.

CADDY, J. F.
1977. Approaches to a simplified yield-per-recruit model for Crustacea, with particular reference to the American lobster, *Homarus americanus*. Can. Fish. Mar. Serv. Manuscr. Rep. 1445, 14 p.
1979. Notes on a more generalized yield per recruit analysis for crustaceans, using size-specific inputs. Can. Fish. Mar. Serv. Manuscr. Rep. 1525, 7 p.

ENNIS, G. P., AND S. A. AKENHEAD.
1978. A model and computer program used to assess yield per recruit in Newfoundland lobster stocks. CAFSAC (Can. Atl. Fish. Sci. Advis. Comm.) Res. Doc. 78/30, 13 p.

HERRICK, F. H.
1911. Natural history of the American lobster. Bull. [U.S.] Bur. Fish. 29:149-408.

PERKINS, H. C.
1971. Egg loss during incubation from offshore northern lobsters (Decapoda: Homaridae). Fish. Bull., U.S. 69:451-453.

SAILA, S. B., J. M. FLOWERS, AND J. T. HUGHES.
1969. Fecundity of the American lobster, *Homarus americanus*. Trans. Am. Fish. Soc. 98:537-539.

SQUIRES, H. J.
1970. Lobster (*Homarus americanus*) fishery and ecology in Port au Port Bay, Newfoundland, 1960-65. Proc. Natl. Shellfish. Assoc. 60:22-39.

SQUIRES, H. J., G. P. ENNIS, AND G. E. TUCKER.
1974. Lobsters of the northwest coast of Newfoundland, 1964-67. Proc. Natl. Shellfish. Assoc. 64:16-27.

G. P. ENNIS

Research and Resource Services
Department of Fisheries and Oceans
P.O. Box 5667, St. John's, Newfoundland A1C 5X1

MORTALITY OF SEABIRDS IN HIGH-SEAS SALMON GILL NETS[1]

Since 1952, the Japanese have operated a large salmon driftnet fishery in the northern North Pacific Ocean and Bering Sea. This fishery is divided into two components: the high-seas mothership fleet, which consists of several processing ships and their numerous, smaller catcher boats that remain at sea during the entire fishing season, and the land-based fleet, which consists of independent fishing boats that catch and store their own fish and return to Japan at more fre-

[1]Contribution No. 224 of the Point Reyes Bird Observatory.

quent intervals (Sanger 1976; Fredin et al.[2]). A similar fishery in the North Atlantic between 1965 and 1976 was responsible for the deaths of large numbers of the thick-billed murre, *Uria lomvia*, and significant reductions in its breeding populations (Tull et al. 1972). Recent work in the North Pacific and Bering Sea by Sano (1978) and King et al. (1979) indicated that large numbers of seabirds are killed annually in the Japanese salmon fishery also.

Previous estimates of seabird mortality resulting from the Japanese high-seas and land-based gill net fisheries were based on data gathered from research nets only (e.g., Sano 1978; King et al. 1979). These nets include both smaller and larger mesh sizes than nets used in the commercial fishery. We wished to investigate if mesh size influenced bird mortality rates, and if so, to reassess the impact of gill net fisheries on seabird mortality. Since previous estimates of the total bird catch were based on data averaged over broad regions, we also investigated the geographic variation in catch rates to determine whether in some areas they could potentially be having an important impact on local bird populations.

[2]Fredin, R. A., R. L. Major, R. G. Bakkala, and G. K. Tanonaka. 1977. Pacific salmon and the high seas salmon fisheries of Japan. Processed Rep., 324 p. Northwest and Alaska Fisheries Center, NMFS, NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

Methods

We participated in cruises aboard Japanese research vessels during 1978 and 1979 as shown in Figure 1. The *Oshoro Maru* and *Hokusei Maru* deployed research nets and the *Hoyo Maru No. 67* deployed a small series of research nets between two extensive spans of commercial nets. Research and commercial nets differ significantly only in the variety of mesh sizes used. In this study the mesh sizes in the research nets ranged 37 to 233

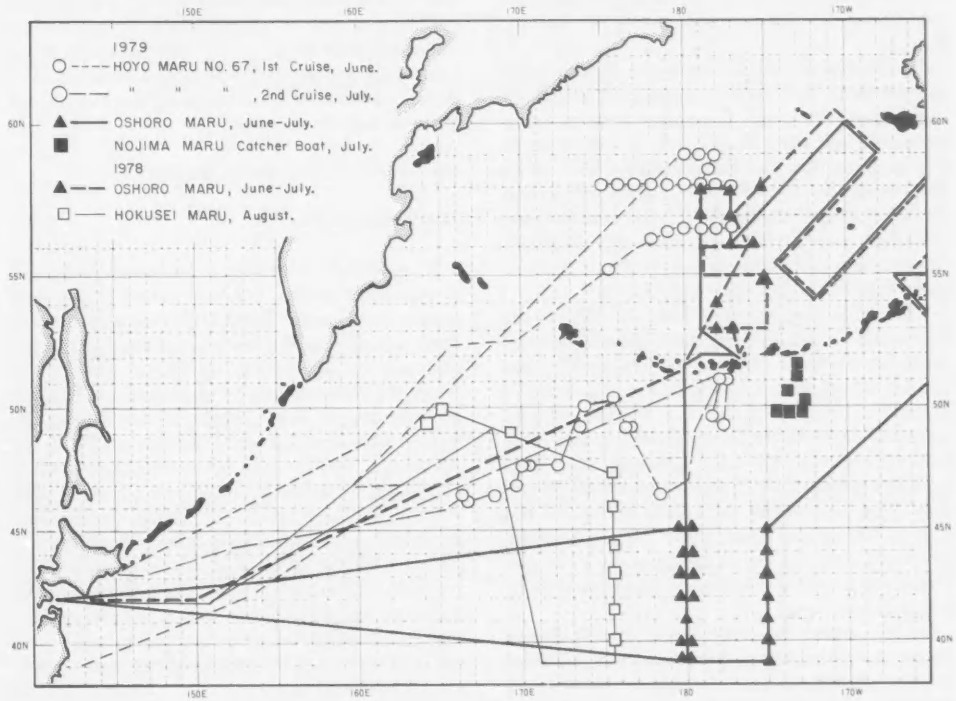

FIGURE 1.—Cruise tracks (lines) and net setting stations (symbols) where observations were made in 1978 and 1979.

mm but the commercial nets were limited to meshes ranging 110 to 130 mm. In 1979 we also obtained some data from commercial catcher boats of the mother ship *Nojima Maru*, but these were used only in determining geographical differences in catch rates. Nets were set at 16:30 h and hauled at 02:30 h on *Hoyo Maru No. 67*, similarly to commercial boats; on other cruises deployment and retrieval were at 18:00 h and 03:00 h. Nets consisted of panels, called tans, 50 m by 6 m deep that were sewn together in series, with floats attached to the topline and lead weights attached to the bottom line of each panel. The stretched mesh thus hung vertically like a curtain from the sea surface down to a depth of 6 m. A commercial net was usually about 15 km long, while those on our vessels were about 6.5 km (130 tans). A commercial fleet of 45 catcher boats (plus a mother ship) deployed its nets in parallel lines on a grid, each net about 5 nmi from neighboring ones. For several sets in the central Bering Sea, *Hoyo Maru No. 67* fished within the configuration of a commercial fleet. A complete review of the Japanese drift gill net fishery is contained in Fredin et al. (footnote 2).

On all cruises except that of the *Nojima Maru* catcher boats, we noted entangled birds as the nets were being retrieved. Carcasses from the first cruise of *Hoyo Maru No. 67* were saved by Jones, frozen, shipped to the United States, and, along with those from *Nojima Maru*, were later identified by Ainley; those from other cruises were identified immediately by Ainley and DeGange. On most sets the mesh size and the depth at which birds were entangled were recorded.

Using data from the *Hoyo Maru No. 67* and the *Nojima Maru* catcher boats (see Figure 1), we compared catch rates to distance south of the Aleutian Islands. Data from *Oshoro Maru* and *Hokusei Maru* were not used because they did not use commercial nets. However, a comparison of catch rates to the distance north of the Aleutians used data exclusively from *Oshoro Maru* because we had no data from commercial nets close enough to the islands. The shape of the regression curve would not be affected but the asymptotes would be displaced downward due to the low catch rates of the research nets used.

On two cruises in 1979, Ainley and DeGange censused seabirds that occurred within 300 m of one forequarter of the ship whenever we steamed at 9-12 kn during daylight; birds circling or following the ship were ignored. Distance traveled during a given time period (a transect) multiplied by the 300 m transect width provided an estimate of ocean area surveyed. Area divided into the number of birds counted resulted in an index of bird density per square kilometer. For 16 sets on the July cruise of *Hoyo Maru No. 67* and 5 sets on the 1979 cruise of *Oshoro Maru*, densities of netable seabird species (i.e., those caught during the cruises) were correlated to the number caught per tan (110-130 mm mesh only) at each set. Density indices at netting areas were averages of the counts immediately before arrival at and another after departure from the netting site. Only five of *Oshoro Maru*'s sets were used because other studies took her far away from netting areas at very low speed before transits at cruising speeds began. We equilibrated our estimates of bird density based on simultaneous but independent counts made aboard *Oshoro Maru*, 25-27 July 1979.

In the following discussions oceanographic regions are approximate because they are based on geographic locality as shown in Favorite et al. (1976), and not on sophisticated oceanographic measurements taken at the time of bird observations. Hourly sea-surface temperatures, however, did aid somewhat in confirming the boundaries between certain domains.

Results and Discussion

Species Observed

We recorded 31 species of seabirds during our at-sea observations but only 15 of these were caught in the nets (Table 1). For certain species, their pelagic distribution was reflected in the gill net catch by statistically significant correlations ($P<0.05$) between density estimates and number of birds caught. For example, in the Bering Sea and in Western Subarctic waters south of the Aleutians, the short-tailed shearwater greatly outnumbered the sooty shearwater, both in density and in the gill nets, but farther south to just north of the Subarctic Front their numerical importance in the catch and in the censuses was reversed. Several other species also showed differences in their distributions, for example, ancient murrelet and crested auklet.

A bird's foraging methods influenced its susceptibility to being caught (Table 2). Of the 13 species we observed that feed beneath the sea surface by diving or pursuit plunging (see Ainley 1977 for

TABLE 1.—Density indices ±SD and number caught per tan ($\times 10^{-3}$) in parentheses for netable seabird species in different oceanographic areas; the number of ½-h transects are shown below each area name.

Species	Transitional Domain (27)	W. Subarctic Gyre (36)	Alaskan Stream (24)	Bering Gyre (97)	Bering Current (8)
Laysan albatross,	0.1±0.1	0.1±0.1	0.1±0.1		0.1±0.2
Diomedea immutabilis	(2.0)	(1.0)			
Northern fulmar,	3.2±5.6	1.8±1.4	.8±0.4	.3±.3	.6±.3
Fulmarus glacialis		(3.0)			
Flesh-footed shearwater,[1]	.1				
Puffinus carneipes	(0.3)				
Sooty shearwater, [1,2]	.4±.8	.1			
P. griseus	(18.0)	(2.0)	(.2)		
Short-tailed shearwater, [1,2]		11.7±15.6	10.0±13.5	.8±1.2	5.5±1.9
P. tenuirostris	(0.6)	(17.0)	(66.)	(3.0)	(60.0)
Fork-tailed storm-petrel,	1.9±1.8	3.1±2.8	2.6±1.1	1.5±1.0	2.3±1.2
Oceanodroma furcata		(8.0)		(.6)	(2.0)
Common murre,[1]		.1		.1	
Uria aalge				(.3)	
Thick-billed murre,[1,2]		.1±.2	.2±.4	.1±0.2	.5±.2
U. lomvia		(2.0)	(5.0)	(4.0)	(12.0)
Ancient murrelet,[1]				.1±.4	.8±.8
Synthliboramphus antiquus				(1.0)	(2.0)
Parakeet auklet,[1]			.1	.1	
Cyclorrhynchus psittaculus			(0.2)		
Cassin's auklet,[1]					
Ptychoramphus aleuticus			(.2)		
Least auklet,[1]			.2±.6	3.3±4.3	1.2±1.6
Aethia pusilla		(1.0)			
Crested auklet,[1]			.1	.7±1.6	.7±.8
A. cristatella		(2.0)	(1.0)		
Rhinoceros auklet,[1]	.1±.2				
Cerorhinca moncerata			(0.2)		
Horned puffin,[1]	.2±.2	.4±.5	.3±.4	.4±.5	3.9±2.4
Fratercula corniculata	(.6)	(5.0)	(3.0)	(2.0)	(2.0)
Tufted puffin,[1]	.2±.2	.4±.5	.3±.4	.4±.5	3.9±2.4
Lunda cirrhata	(3.0)	(8.0)	(18.0)	(7.0)	(6.0)

[1]Species that feed principally beneath the sea surface by diving or pursuit plunging.
[2]For correlation between density index and catch rate, $P < 0.05$; Spearman's rank correlation.

TABLE 2.—The number of individuals by species caught in net meshes of various sizes (stretched).[1]

Species	Mesh size (mm)																
	37	42	48	55	63	72	82	93	105	112-115	118-121	130	138	157	179	204	233
Laysan albatross		2								2	1						
Northern fulmar										9			1				
Flesh-footed shearwater														1			
Short-tailed shearwater			1			1		1	14	106	11	15		1			
Sooty shearwater		1			1		3	4	2	23	12	4	3	3	2	2	
Fork-tailed storm-petrel							1			11							
Common murre										1							
Thick-billed murre							2		1	25	2	1	1	1	1		
Ancient murrelet							1	1			1						
Cassin's auklet								1									
Horned puffin							1			8			2				
Tufted puffin								4	2	42	4	1	3	1		2	
Least auklet										1							
Crested auklet							1			2	1						
Total	0	3	1	0	1	1	9	11	19	230	32	21	10	7	3	4	0
Tans set	162	162	489	495	495	495	495	495	495	7,303	3,035	674	495	495	155	162	27
Birds/tans set	0.00	0.019	0.002	0.00	0.002	0.002	0.018	0.022	0.038	0.031	0.011	0.031	0.020	0.014	0.019	0.025	0.00
$\bar{X}$ catch rate			[2]0.003				[3]0.020				[4]0.026				[3]0.018		

[1]Does not include thick-billed murre of *Hoyo Maru* set 17 or ancient murrelets of set 20; net retrieval was not observed.
[2]Significantly fewer than the other three classes ($P<0.01$; Sokal and Rohlf 1969:608).
[3]No significant difference in catch rates ($P>0.05$).
[4]Significantly higher than the other three classes ($P<0.05$).

definitions), all were entangled at least once and were also entangled deeper in the nets than just the upper meter (Good and Ainley unpubl. data). Only 3 (17%) of the other 18 species we observed at sea were caught in the nets. Almost all of these feed at the surface by scavenging, dipping, or by shallow plunges; the 3 caught were the most abundant scavengers of the area: laysan albatross, northern fulmar, and fork-tailed storm-petrel. Direct observations of their behavior and examina-

tion of their stomach contents (Good and Ainley unpubl. data) indicated that entanglement occurred as they attempted to eat fish caught in the net. A much smaller percentage (ca. 5%) of shearwaters (pursuit plungers) were caught while eating entangled fish, but probably none of the diving species (murres, puffins, etc.) scavenged from the nets (confirmed by stomach contents).

Rates of Entanglement

We tabulated birds by the mesh size in which they were entangled (Table 2). Catches in 112-115 mm meshes were combined as were those in 118-121 mm meshes. Not included were birds caught by commercial boats because we were not sure that all specimens reached us. Catch rates for six mesh sizes <82 mm were negligible, but rates for 106-138 mm meshes, including those used in the commercial salmon fishery (121-138 mm) (Fredin et al. footnote 2) were statistically greater than for the other categories. In 157-233 mm meshes, with or without the 233 mm mesh—no birds caught and only 27 tans set—the rate was similar to that for 82-93 mm meshes. Based on those results, we excluded from further analysis birds caught with ≤82 mm meshes.

The number of birds caught per tan was directly proportional to the density of netable species present at the netting locality ($r = 0.7154$, $P<0.01$, t-test). The correlation was improved ($r = 0.7604$) when catch rates were adjusted for the actual amount of time the nets were deployed (i.e., birds/tan per hour deployed). The correlation would probably be improved even more if density indices were adjusted for the detectability of birds. For instance, tufted puffins on the water in the outer third of the 300 m count zone would probably not have been seen, especially in rough seas. The difficulty in detecting puffins might account for the lack of correlation between density indices and catch rates in Table 1, where significant correlations existed for more easily observed species.

The facts that bird densities differed geographically (or oceanographically; Table 1) and that catch rates were proportional to bird density led us to look for geographic differences in catch rates. In the northern North Pacific, the mean number of birds caught per tan increased with latitude. Rates were lowest, varying 0.00-0.03 bird/tan, between lat. 39° and 43° N (Subarctic Front and the Transitional Domain); were slightly higher, 0.03-0.08, between lat. 44° and 48° N (Western Subarctic Domain); and were highest, 0.04-0.51, between lat. 49° and 51° N (Alaskan Stream). In that part of the Bering Sea sampled, the number of birds caught per tan increased with decreasing latitude. In the central Bering Sea (Bering Sea Gyre) catch rates were low, ranging 0.01-0.05, and were higher at the gyre periphery. Farther south in the extreme periphery of the gyre, the Bering Current, catch rates ranged 0.04-0.16. These rates were consistent with the relative differences in bird densities in these oceanographic regions (Table 1). Greater bird densities in the Alaskan Stream and Bering Current were due to the more productive waters there and to closer proximity to the Aleutian Islands where murres, puffins, and several other netable species breed. In fact, as a direct function of distance, within 200 nmi of the Aleutians catch rates varied logarithmically ($P<0.01$; Figure 2). Rates were especially high within 50-75 nmi of the islands, where most of the murres and puffins in net samples were breeding adults (based on the presence of incubation patches). Most of those caught in the Bering and Western Subarctic Gyres and Transitional Domains were immature.

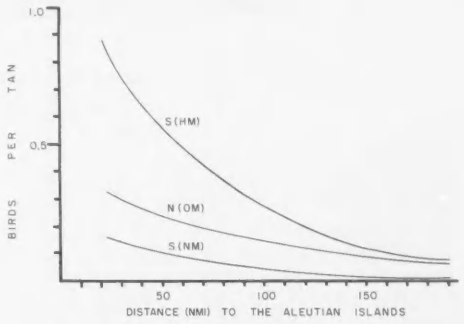

FIGURE 2.—Logarithmic relationships between bird catch rates and distance to the Aleutian Islands within 200 nmi, 1979: S(HM) = *Hoyo Maru* stations south of the islands ($r = 0.9167$, $P < 0.01$; $y = 0.74 - 0.13 \ln x$), S(NM) = Nojima Maru stations south of the islands ($r = 0.9186$, $P < 0.01$; $y = 0.36 - 0.07 \ln x$), and N(OM) = *Oshoro Maru* stations north of the islands ($r = 0.9869$, $P < 0.01$; $y = 0.74 - 0.13 \ln x$); see Figure 1 for station localities.

Overall Seabird Mortality

The above estimates of catch rates, if applied to the commercial fishery, are minimal for two

reasons: most could be increased by >30% to account for the higher catch rates of nets with commercial size meshes (Table 2), and our estimates of commercial catch rates did not account for birds that dropped from the net before its retrieval. On the July cruise of *Hoyo Maru No. 67*, 3 shearwaters (of 6 caught) and 1 puffin (of 12 caught) dropped from the net when it was stretched taut in the retrieval process. On that cruise, 13% of the dead birds would not have been counted if only figures on the number of dead birds reaching the deck had been used as in other estimates of catch rates. Similarly, on cruises of the *Hokusei Maru* in 1978 and that part of the *Oshoro Maru* cruise south of the Aleutian Islands in 1979, 1 of 9 (11%) and 3 of 66 birds (5%), respectively, dropped out during net retrieval.

A valuable result of this study is the more realistic estimate of bird catch rates, compared with previous estimates (Sano 1978; King et al. 1979; Japanese Fishery Agency 1977 in DeGange[3]; DeGange footnote 3). Prior estimates agreed but were too low because they were based on research gear and the assumption that catch rates were the same regardless of mesh size, and they did not give enough attention to geographic differences in catch rates. They derived an overall mean value for birds caught per tan fished which dilutes considerably the high catch rates in certain areas. DeGange's (footnote 3) analysis, representative of earlier mortality estimates, derived a total of about 112,500 birds caught annually in the mothership fishery. We propose that a figure of 205,000, an increase of about 82%, is more realistic (Table 3). If our estimate were increased by an additional 30% to adjust for the high catch rates of commercial meshes, the resultant figure of 266,500 birds is 136% higher.

The demonstration that bird catch rates increase logarithmically as distance to the Aleutian Islands decreases, and are generally higher in productive waters, is especially important. More observations are needed on catch rates in commercial nets to clarify the critical distance, but fishing at some distance within 50-75 nmi of the islands would severely reduce breeding populations of certain diving birds. This is precisely what happened when a salmon gill net fishery off Greenland was concentrated too near to murre breeding sites (Tull et al. 1972). In that fishery, 88% of the estimated 350,000-500,000 thick-billed murres caught per year were entangled in nets set <30 nmi from the coast. Other species, however, showed different distance-to-coast relationships; for example, 36% of the black guillemot, *Cepphus grylle*, were entangled <12 nmi from the coast, 80% of the greater shearwater, *Puffinus gravis*, were caught between 12 and 30 nmi, and 75% of the dovekie, *Plautus alle*, were caught between 12 and 60 nmi (50% at 30-60 nmi; Christensen and Lear (1976)).

In the North Pacific where the salmon driftnet fishery is much larger than the one in Greenland was, it is likely that gill netting has also been concentrated near bird breeding sites. In a sample of years for which data on the number of tans fished were available to us (n = 12 during 1955-69 International North Pacific Fisheries Commission[4]), 44.4% of effort east of long. 170° E, or several million tans annually, was concentrated in the six 2° × 5° blocks (24 total blocks fished in that area) containing the western Aleutians. Such concentration of effort, coupled with marked geographic differences in bird catch rates, indicates the limitations in estimating the total seabird kill by using statistics averaged over broad areas as attempted by King et al. (1979). Their estimate of 5.0 million birds killed by the entire mothership fishery between 1952 and 1974, based on an average annual mortality of 250,000, is extremely low and should be at least doubled. After all, in the fishing area east of long. 170° E alone, we estimate that at least 4.1 million birds were killed in just the 12 yr mentioned above.

[3]D. Gange, A. R. 1978. Observations on the mortality of seabirds in Japanese salmon gill nets made from the OSHORO MARU and HOKUSEI MARU, summer 1978. Unpubl. Rep., 37 p. U.S. Fish Wildl. Serv., Off. Biol. Serv., Anchorage, Alaska.

TABLE 3.—A comparison of bird catch in the 1978 mothership salmon fishery using two methods of catch rate estimation; the DeGange (text footnote 3) method is typical of all previous types of estimation.

2° N × 5° E Block	Tans fished[1]	Bird per tan		Total birds caught		
		DeGange	This report	DeGange	This report	Percent increase
50-165	34600	0.036	0.130	1,246	4,498	260
52-165	45800	.036	.130	1,649	5,954	260
48-170	250600	.040	.130	10,024	32,578	220
50-170	939500	.084	.130	78,918	122,135	60
52-170	281500	.053	.130	14,920	36,596	140
54-170	103400	.053	.038	5,480	3,929	−30
56-170	8900	.035	.038	312	338	10

[1]Source of data: International North Pacific Fisheries Commission (text footnote 4).

[4]International North Pacific Fisheries Commission. 1955-79. Catch statistics of Japanese mothership gillnet and land-based driftnet fisheries. Int. North Pac. Fish. Comm. Doc.

Acknowledgments

We thank the Fishery Agency of Japan for allowing our participation in 1978 and 1979 cruises. The cooperation and hospitality extended to us was admirable. R. L. Brownell, Jr., National Fish and Wildlife Laboratory, U.S. Fish and Wildlife Service, arranged the participation of Ainley and DeGange, and Ainley's efforts were funded by that office. Help in the laboratory was contributed by A. E. Good. The comments by R. L. Brownell, W. B. King, and two anonymous reviewers greatly improved the manuscript.

Literature Cited

AINLEY, D. G.
1977. Feeding methods in seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. *In* G. A. Llano (editor), Adaptations within Antarctic ecosystems, p. 669-685. Gulf Publ., Houston.

CHRISTENSEN, O., AND W. H. LEAR.
1976. Bycatches in salmon drift-nets at West Greenland in 1972. Medd. Grønl. 5(205):1-29.

FAVORITE, F., A. J. DODIMEAD, AND K. NASU.
1976. Oceanography of the subarctic Pacific region, 1969-71. Int. North Pac. Fish. Comm., Bull. 33:1-187.

KING, W. B., R. G. B. BROWN, AND G. A. SANGER.
1979. Mortality to marine birds through commercial fishing. *In* J. C. Bartonek and D. N. Nettleship (editors), Conservation of marine birds of northern North America, p. 195-200. U.S. Fish Wildl. Serv., Wildl. Res. Rep. 11.

SANGER, G. A.
1976. Update on seabird mortality from salmon driftnets. Pac. Seabird Group Bull. 3(2):30-32.

SANO, O.
1978. Seabirds entangled in salmon driftnets. Enyo 30:1-4.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry; The principles and practice of statistics in biological research. W. H. Freeman, San Franc., 776 p.

TULL, C. E., P. GERMAIN, AND A. W. MAY.
1972. Mortality of Thick-billed Murres in the West Greenland Salmon Fishery. Nature (Lond.) 237:42-44.

DAVID G. AINLEY

Point Reyes Bird Observatory
Stinson Beach, CA 94970

ANTHONY R. DEGANGE

Office of Biological Services
U.S. Fish and Wildlife Service
Portland, OR 97232

LINDA L. JONES
RICHARD J. BEACH

Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA
7600 Sand Point Way, Seattle, WA 98115

HISTOCHEMICAL INDICATIONS OF LIVER GLYCOGEN IN SAMPLES OF EMACIATED AND ROBUST LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

On the basis of histological criteria (O'Connell 1976), 8% of northern anchovy, *Engraulis mordax*, larvae from special net tows taken in the Southern California Bight in March 1977 were found to be in starving condition (O'Connell 1980). Almost three-quarters of the larvae that showed signs of starvation were concentrated in 4 of the 64 net tow samples. The present report compares the amount of glycogen in livers of additional larvae drawn from these four samples to that in the livers of larvae from samples taken in the same area, which contained robust larvae almost exclusively.

Glycogen, which is stored in the liver and transformed to glucose as needed to maintain an adequate blood sugar level, is the most immediately available of the three energy sources, glycogen, lipid, and protein (Love 1974). It is known to virtually disappear from the livers of many teleosts after only a few days of starvation (Black et al. 1966; Inui and Ohshima 1966; Bellamy 1968), but fish generally live long beyond the depletion of liver glycogen, maintaining the blood sugar level by gluconeogenesis (Love 1974; Cowey and Sargent 1979). However, there are also teleosts in which liver glycogen does not decline sharply at the onset of starvation, although gluconeogenesis does increase (Cowey and Sargent 1979). Thus abundance of liver glycogen cannot be considered a dependable indicator of starvation in teleosts, at least not for adult stages.

Postyolk-sac larval stages, which first exhibit stained liver glycogen about the time yolk is depleted, are more likely to show a drop in liver glycogen at onset of starvation. First feeding northern anchovy larvae die after only a few days of starvation (O'Connell 1976), indicating that reserves are limited. Lipid reserves, for example, are known to be negligible in early postyolk-sac herring and plaice larvae (Ehrlich 1974), and even at the relatively large size of 35 mm SL northern anchovy larvae survive starvation conditions for only 2 wk, on the average, during which time lipid reserves are severely depleted (Hunter 1976). Presumably liver glycogen declines sharply before lipid reserves are depleted in these early stages.

The estimates of glycogen reserves in the works cited above, and in many others, are derived from weight-based biochemical determinations, which

is not a feasible approach for small larvae already preserved as part of plankton samples at sea. A histochemical approach is feasible, however, and we elected the periodic acid-Schiff (PAS) procedure, which has largely superseded other histochemical tests for glycogen (Davenport 1960).

Cardell et al. (1973) showed good correlation of PAS staining reactions with biochemical determinations of liver glycogen for the rat. Glycogen decreased from about 9% of liver wet weight to 0.7% after 1 d of fasting and to 0.4% after 3 d. At the start of the experiment all hepatocytes had dense masses of intensely stained glycogen. As the fasting period lengthened to 2 and 3 or more days, the masses decreased in size, number, density, and stain intensity, and the number of cells showing glycogen decreased markedly. Presumably such differences in staining reaction in livers of northern anchovy larvae would be an indication of differences in glycogen reserves.

Materials and Methods

In the laboratory, 49 larvae in the size range 3.5-11 mm SL were selected by random dipping from about half of the 37 nearshore net tow samples that showed larvae of generally good histological condition from the March 1977 cruise (O'Connell 1980). Forty-one larvae were selected, also by random dipping, from three of the four nearshore tows containing abundant larvae in generally poor histological condition. An additional dozen larvae were selected from three of the offshore tows.

All larvae had been fixed at time of capture in Bouin's fluid and stored in 70% ethyl alcohol. They were subsequently dehydrated in *n*-butyl alcohol, embedded in paraffin, sectioned sagittally and stained by the PAS method (Preece 1965). We did not subject the material used in this study to diastase digestion tests but feel confident that the red coloration in the livers indicates glycogen. Glycogen gives one of the stronger reactions to the PAS stain (Lillie and Fullmer 1976), and Cardell et al. (1973) established with diastase controls that the PAS-positive material in the livers of rats was glycogen. The diastase test essentially distinguishes between glycogen and mucins (Preece 1965), some of which show strong PAS reactions, but these occur primarily in the integument and epithelia of the digestive tract and various glands of animals (Lillie and Fullmer 1976).

After staining, slides were randomized with their identities concealed and then rated by microscope examination. Each of two observers rated each specimen as High, Medium, or Low, depending on the degree and extent of red coloration in the liver. The Low grade was assigned when livers showed virtually no red color, the High grade when color was strong and widespread. The Medium grade was assigned when color was light and scattered, or irregular. The two readers disagreed on a little >12% of the larvae but never by more than one grading step. These differences were reconciled by reexamination and discussion.

No attempt was made to characterize the specimens stained by the PAS procedure as robust or emaciated on the basis of histological factors per se. There was the possibility that the PAS procedure would be less precise and consistent than the previously used hematoxylin and eosin stain in demonstrating cell and tissue components other than polysaccharides.

Study of material from the sea samples was preceded by analysis of 99 specimens from groups of larvae that were fed or starved in the laboratory. Fixation, staining, and microscope analysis were exactly as outlined above, except that the laboratory material was held in 70% ethyl alcohol for only a few days before dehydration and embedding. Reader disagreement was 9% on the laboratory material.

The larvae obtained from laboratory containers ranged from 5- to 26-d-old. The rotifer *Brachionus plicatilis* was introduced into containers as food at a density of 40 to 60/ml when the larvae were 3-d-old and maintained above 30/ml by additions as needed. The smaller *Gymnodinium splendens* was included as a starting food at the outset, but was not afterwards maintained. Northern anchovy larvae require *Brachionus* at densities of at least 10 to 20/ml to survive and grow well in laboratory containers for the first weeks of life (Theilacker and McMaster 1971).

Food was withheld from two containers, and specimens from these were sacrificed on the first and second day after yolk exhaustion. Starvation at more advanced ages was accomplished by removing the food from selected containers 2 to 4 d before the larvae were sacrificed. Food was removed with a siphon filter devised by P. Paloma for the purpose. A typical air-driven aquarium siphon was enclosed in an 8.89 cm (3.5 in) diameter perforated plastic cylinder covered by nylon netting with 0.333 mm mesh openings, which allowed food organisms but not fish larvae to pass

towards the siphon. The outflow tube of the siphon recurved after passing through the top stopper of the cylinder and terminated in a small perforated cylinder above the water surface. Inside the small cylinder the outflow tube opened into a bag of nylon netting with 0.024 mm mesh openings, which removed food organisms and allowed water to return to the rearing container by dropping onto a small glass plate at the water surface.

Operating at a flow rate of 3 l/h in containers of 12.6 l capacity, the filter reduced *Brachionus* populations ranging from 40 to 100/ml at the start to 7/ml in 1 d, 3/ml in 2 d, and considerably < 1/ml in 3 d. It reduced populations of *Gymnodinium* at about the same rate. At the filtering rate of 3 l/hr, larvae close to the submerged barrier cylinder did not appear to be disturbed.

Results

Laboratory material showed good association between food treatment and PAS glycogen rating over the entire length range involved, 3 to 15 mm SL. The larvae were divided into two groups, those smaller than the median (6.4 mm SL) and those larger than the median. For both size groups, as for all larvae pooled, the majority of High ratings occurred in the "fed" category and the majority of Low ratings occurred in the "starved" category (Table 1). It is noteworthy that only 4 larvae among the 45 from starvation treatments received High ratings. Three of these were from the oldest age group, 26 d (starved 3 d), and were in fact three of the four largest larvae in the entire starved contingent. Examples of stained liver sections representing High, Medium, and Low glycogen ratings are shown in Figure 1.

Larvae from the laboratory trials were fixed in Bouin's solution, as described earlier, to be comparable to the Bouin-fixed sea samples, but a few other fixatives were tested as a matter of perspective. Gendre's solution (Preece 1965) gave somewhat better results than Bouin's, but 10% alcoholic Formalin,[1] which is theoretically a better fixative for preserving glycogen (Davenport 1960; Preece 1965), gave the best results. Some specimens fixed in alcoholic Formalin from fed containers had most hepatocytes solidly filled with deep red color (Figure 1). Presumably more of the glycogen present in the livers at termination was retained with this fixation. However, integrity of cells and tissues of the larvae was not well preserved in alocholic Formalin.

High, Medium, and Low ratings for the ocean-caught larvae (Figure 2) reflect essentially the same levels of staining intensity as for laboratory material. Ocean samples show an appreciably higher proportion of Medium ratings than the laboratory material, but nevertheless exhibit some association between glycogen rating and histological characterization of the samples from which the larvae were drawn (Table 2). However, the association occurs only among the smaller larvae, as indicated by comparing the distributions for larvae smaller and larger than the median, 6.9 mm SL. The smaller larvae show a relatively good proportion of High ratings for robust samples and of Low ratings for emaciated samples. The larger larvae do not exhibit this association.

Significance of the various distributions described above is indicated by X^2 values (Table 3) calculated for each of the six pairs of columns (treated as 2×3 contingency tables) from Table 1 and 2. All three X^2 values for the laboratory material clearly reject the null hypothesis, i.e., that there is no association between the two classifications, food treatment and liver glycogen rating. For the ocean material the null hypothesis is rejected only for small larvae, indicating

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Distribution of High, Medium, and Low glycogen ratings, based on PAS staining intensity in livers of northern anchovy larvae fed or starved in the laboratory.

	<6.4 mm SL		≥6.4 mm SL		Pooled	
Glycogen rating	Fed	Starved	Fed	Starved	Fed	Starved
High	14	1	25	3	39	4
Medium	2	7	3	4	5	11
Low	8	18	2	12	10	30

TABLE 2.—Distribution of High, Medium, and Low glycogen ratings, based on PAS staining intensity in livers of northern anchovy larvae from ocean samples showing either generally robust condition or generally emaciated condition. Condition of samples is based on a previous histological study of other specimens from the same collection.

	<6.9 mm SL		≥6.9 mm SL		Pooled	
Glycogen rating	Robust	Emac.	Robust	Emac.	Robust	Emac.
High	7	2	9	8	16	10
Medium	17	5	7	10	24	15
Low	4	10	5	6	9	16

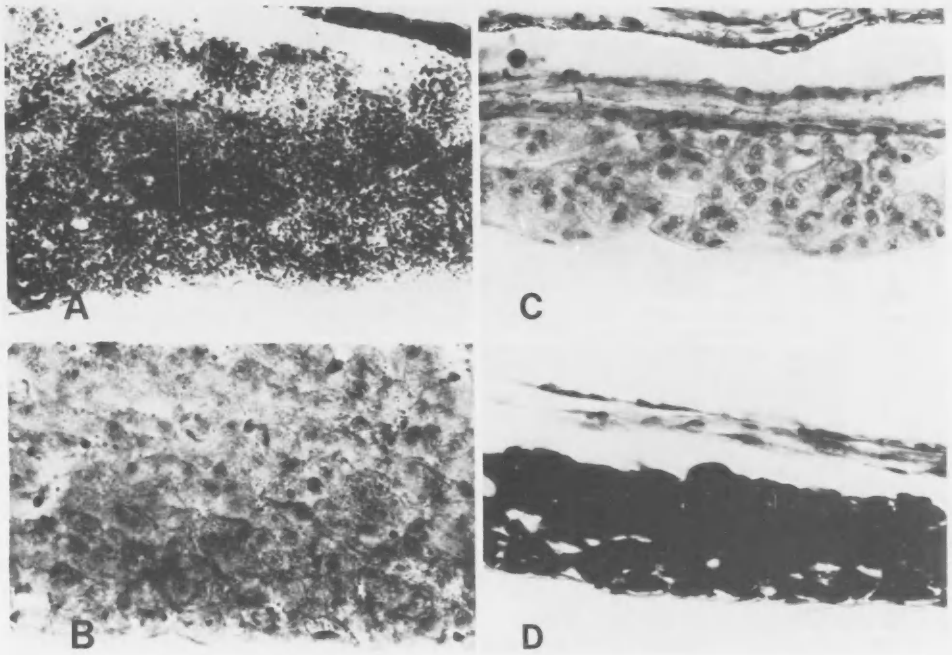

FIGURE 1.—Sagittal sections of livers of northern anchovy larvae from the laboratory, showing the three grades based on intensity of the PAS staining reaction. Except for the nuclei, and occasional portions of other organs, black and the darker shades of grey represent PAS-positive red material presumed to be glycogen. All photomicrographs were taken and processed in the same way. All were taken at 787 ×. A. 5.5 mm larva, fed, graded High. B. 5.0 mm larva, starved, graded Medium. C. 6.1 mm larva, starved, graded Low. D. 5.2 mm larva, fed, graded High. The first three were fixed in Bouin's fluid, but the fourth was fixed in 10% alcoholic Formalin and showed a very intense staining reaction.

TABLE 3.—X^2 and mean contingency square (X^2/n) values for the association between PAS glycogen rating and food treatment for the arrays of larvae shown in Table 1 (laboratory) and Table 2 (ocean). Each set of values is for a 2 × 3 contingency table with (n) larvae and 2 df. In each group, small larvae are those below, and large larvae those above, the median standard length.

Contingency set	n	X^2	P	X^2/n
Laboratory:				
Small larvae	50	17.84	0.001	0.36
Large larvae	49	23.28	.001	.48
Pooled	99	40.13	.001	.41
Ocean:				
Small larvae	43	9.74	.01	.22
Large larvae	43	.47	NS	.01
Pooled	86	4.73	NS	.05

that only for the lower part of the length range is there a meaningful association between treatment (histological characterization of the samples from which larvae were drawn) and liver glycogen rating. As already mentioned, the relevant association is High ratings with samples of generally robust histological condition, and Low ratings with samples of generally emaciated condition. The mean square contingency values (X^2/n) indicate the extent to which the association for small larvae from the ocean is weaker than those from the laboratory.

The dozen larvae from the offshore samples, not included in the above analysis of inshore larvae, showed relatively high liver glycogen ratings. They were almost equally divided among three tows, each of which was taken between 0300 and 0400 h on a different day and contained larvae in a different part of the size range. There were no Low liver glycogen ratings among them. Ratings were largely Medium for the small to medium standard lengths (3.4-7.8 mm) and High for the largest larvae (8.0-9.2 mm). These High ratings, moreover, represent the most intensely PAS

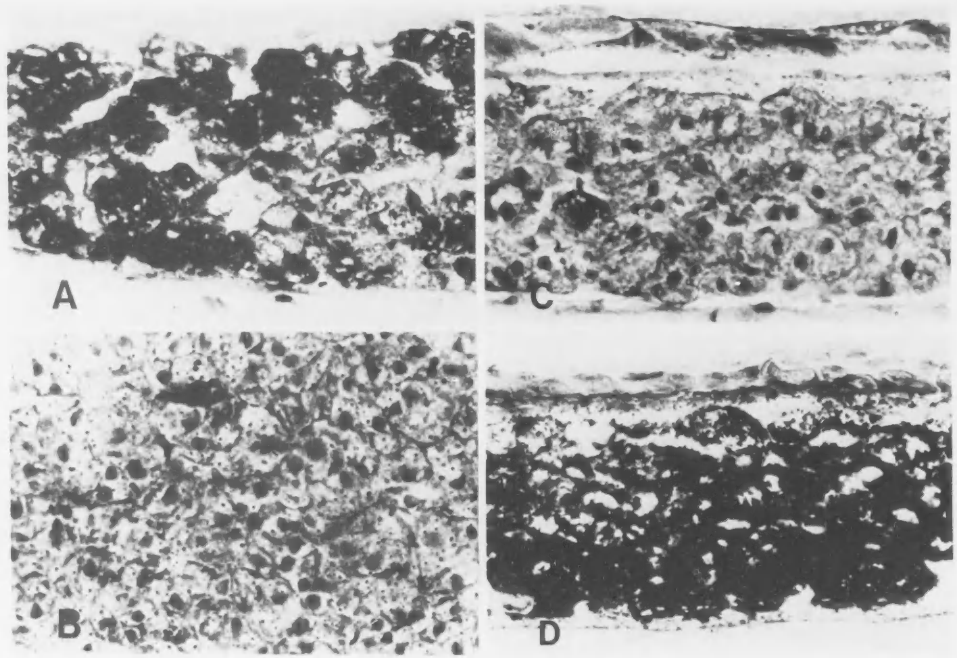

FIGURE 2.—Sagittal sections of livers of anchovy larvae from ocean samples, showing the three grades based on intensity of the PAS staining reaction. Darker shades represent PAS positive red material. Photomicrographs were taken and processed in the same way as those in Figure 1. All were taken at 787 ×. A. 6.2 mm larva, robust sample, graded High. B. 6.3 mm larva, emaciated sample, graded Medium. C. 6.0 mm larva, emaciated sample, graded Low. D. 9.2 mm larva, robust sample, graded High. Whereas the first three are from inshore samples, the fourth is from an offshore sample that produced the most intense staining reactions of all ocean samples.

stained livers in the entire set of ocean specimens (Figure 2).

Discussion

This study was undertaken to determine whether a histochemical test for glycogen in the liver would indicate the occurrence of starvation among northern anchovy larvae from the sea. The results show that variation in glycogen concentration was lower, on the average, for larvae from sea samples classified in a previous histological study (O'Connell 1980) as generally emaciated, than for larvae from samples classified as generally robust. However, the difference was not as strong as it was for larvae that were fed or starved in the laboratory.

Glycogen stored in the livers of fishes can be severely reduced by sustained swimming activity at moderate levels (Miller et al. 1959; Pritchard et al. 1971) or by starvation (Love 1974). It may also undergo some change relative to daily cycles of feeding and nonfeeding. There is no reason to believe that undue exercise was involved in the present case, and the data do not indicate a relation between glycogen rating and hour of capture. Starvation therefore seems the most likely explanation of the low levels shown by certain samples studied here, and this is supported by the relation of glycogen level to plankton volume, a not unreasonable index of food availability in the sea. For those sea samples characterized as emaciated and showing low liver glycogen reserves, the plankton volumes were among the lowest volumes obtained on the March 1977 cruise (O'Connell 1980). These low plankton volumes can be assumed to represent reduced but not essentially nonexistent food, as does

the starvation treatment in the laboratory. This difference might account for the greater proportion of Medium ratings in the ocean samples, robust as well as emaciated. In any event, a moderate proportion of Medium glycogen ratings for the ocean samples is not inconsistent with the earlier histological assessments. The emaciated samples, for example, contained only 60% larvae showing histological signs of moderate to severe emaciation or starvation (O'Connell 1980).

The apparently higher level of liver glycogen among larvae from offshore samples further indicates that food availability is an important factor governing liver glycogen reserves. The plankton volumes for all offshore samples averaged considerably higher than the plankton volumes for inshore samples (O'Connell 1980). Moveover, the particular offshore sample that produced the larvae with the most intense PAS indications of liver glycogen had the second highest plankton volume of the entire 1977 cruise.

The fact that the association of glycogen reserves and histological condition is evident for only the smaller larvae from the sea might mean that as larvae become larger, they can better tolerate fluctuations in the plankton regime. There was a hint of this also in the laboratory results. Marine fish larvae in general select progressively larger prey and also a broader size range of prey as they grow, and engraulids tend to increase maximum prey size markedly between 8 and 12 mm SL (Hunter in press). Thus a reduction in any part of the crustacean plankton community, but particularly among the smaller organisms, could be detrimental primarily to the smaller larvae.

The PAS staining procedure appears, then, to be capable of demonstrating the presence of starvation effects in a larval fish population. On balance, it is a more readable indicator than the comprehensive histological analysis, but it also provides less information. The level of liver glycogen reflects the status of only the first line of energy reserve, whereas histological analysis, with more varied indications, is more sensitive to the extent of emaciation that has been sustained by the larva. Perhaps both approaches can be applied to the same larva, but if so, the histological indications should be interpreted cautiously. Our impression is that tissues of larvae can be moderately distorted and degraded by the PAS procedure regardless of feeding history or fixative. On the other hand, the histochemical test might provide a sufficient characterization of the condition of larval fish samples for some purposes, especially if fixation is optimized for the preservation of glycogen.

Literature Cited

BELLAMY, D.
1968. Metabolism of the red piranha (*Rooseveltiella nattereri*) in relation to feeding behaviour. Comp. Biochem. Physiol. 25:343-347.

BLACK, E. C., N. J. BOSOMWORTH, AND G. E. DOCHERTY.
1966. Combined effect of starvation and severe exercise on glycogen metabolism of rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 23:1461-1463.

CARDELL, R. R., JR., J. LARNER, AND M. B. BABCOCK.
1973. Correlation between structure and glycogen content of livers from rats on a controlled feeding schedule. Anat. Rec. 177:23-38.

COWEY, C. B., AND J. R. SARGENT.
1979. Nutrition. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology, Vol. VIII, p. 1-69. Acad. Press, N.Y.

DAVENPORT, H. A.
1960. Histological and histochemical technics. Saunders, Phila., 401 p.

EHRLICH, K. F.
1974. Chemical changes during growth and starvation of herring larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 301-323. Springer-Verlag, Berl.

HUNTER, J. R.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull, U.S. 74:81-88.
In press. The feeding behavior and ecology of marine fish larvae. *In* J. E. Bardach (editor), Physiological and behavioral manipulation of food fish as production and management tools. Int. Cent. Living Aquatic Resour. Manage., Manila.

INUI, Y., AND Y. OHSHIMA.
1966. Effect of starvation on metabolism and chemical composition of eels. Bull. Jpn. Soc. Sci. Fish. 32:492-501.

LILLIE, R. D., AND H. M. FULLMER.
1976. Histopathologic technic and practical histochemistry. 4th ed. McGraw-Hill, N.Y., 942 p.

LOVE, R. M.
1974. The chemical biology of fishes. Acad. Press, Lond., 547 p.

MILLER, R. B., A. C. SINCLAIR, AND P. W. HOCHACHKA.
1959. Diet, glycogen reserves and resistance to fatigue in hatchery rainbow trout. J. Fish. Res. Board Can. 16:321-328.

O'CONNELL, C. P.
1976. Histological criteria for diagnosing the starving condition in early post yolk sac larvae of the northern anchovy, *Engraulis mordax* Girard. J. Exp. Mar. Biol. Ecol. 25:285-312.
1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. Fish. Bull., U.S. 78:475-489.

PREECE, A.
1965. A manual for histologic technicians. 2d ed. Little, Brown, Boston, 287 p.

PRITCHARD, A. W., J. R. HUNTER, AND R. LASKER.
1971. The relation between exercise and biochemical changes in red and white muscle and liver in the jack mackerel, *Trachurus symmetricus*. Fish. Bull., U.S. 69:379-386.
THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol. (Berl.) 10:183-188.

CHARLES P. O'CONNELL
PEDRO A. PALOMA

Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 171, La Jolla, CA 92038

INDEX

Fishery Bulletin Vol. 79, 1-4

Acipenser transmontanus—see Sturgeon, white

ADAMS, GARY—see SPOTTE and ADAMS

"Age and growth of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, as indicated by daily growth increments of sagittae," by James H. Uchiyama and Paul Struhsaker 151

Age determination
  sailfish
    morphological features of otoliths 360

AHRENHOLZ, DEAN W., "Recruitment and exploitation of Gulf menhaden, *Brevoortia patronus*" 325

AINLEY, DAVID G., ANTHONY R. DeGANGE, LINDA L. JONES, and RICHARD J. BEACH, "Mortality of seabirds in high-seas salmon gill nets" 800

AL-JUDAIMI, MANAL M., A. K. JAFRI, and K. A. GEORGE, "Proximate composition and nutritive value of some important food fishes from the Arabian Gulf" ... 211

Alaska, lower Cook Inlet
  crab, snow
    description of stage II zoeae from plankton 177

Alaska, northern
  gadids, marine
    trophic importance of, and their body-otolith size relationships 187

Alaska, western
  groundfish
    economic feasibility of domestic harvest 303

Albacore
  growth rates of North Pacific based on tag returns
    covariance analysis 297
    data screening 294
    extended model 299
    grouping of data 295
    growth models 295
    parameter estimation 296
    recovery procedures 294
    standard model 297
    tagging procedures 293

Alewife
  offshore distribution along the Atlantic coast
    commercial catches 481
    depth distribution 482
    seasonal distribution 476

Alewife, anadromous
  difference in sex ratios between the top and bottom of a fishway at Damariscotta Lake, Maine 207

Alopias superciliosus—see Thresher, bigeye

Alosa aestivalis—see Herring, blueback

Alosa pseudoharengus—see Alewife; Alewife, anadromous

AMES, JACK A.—see LOUGHLIN et al.

Amphiprion percula
  responses of northern anchovy to predation by 727

"(An) analysis of catch and effort data from the U.S. recreational fishery for billfishes (Istiophoridae) in the western North Atlantic Ocean and Gulf of Mexico, 1971-78," by Grant L. Beardsley and Ramon J. Conser 49

Anchovy, northern
  burst swimming performance of larvae 143
  feeding selectivity of schools in Southern California Bight
    comparison of feeding selectivity between cruises . 138
    comparison with other studies 140
    evaluation of field method 139
    school characteristics 133
    school feeding 134
  larvae, emaciated and robust
    histochemical indications of liver glycogen in samples 806
  responses to predation by *Amphiprion percula* 727
  spawning energetics of female
    annual fat cycle and spawning 223
    energy budget for female growth and reproduction 224
    energy cost of spawning 221
    spawning frequency and rate of egg maturation .. 218

ANDERSON, JAMES JAY, "A stochastic model for the size of fish schools" 315

ANDRYSZAK, BRYAN L., and ROBERT H. GORE, "The complete larval development in the laboratory of *Micropanope sculptipes* (Crustacea, Decapoda, Xanthidae) with a comparison of larval characters in western Atlantic xanthid genera" 487

Anglerfish
  osteology and relationships of genus *Tetrabrachium*
    comparative osteology of antennarioid families ... 397
    osteology 390
    phylogenetic relationships 412
    systematics 388

"Annual reproduction, dependency period, and apparent gestation period in two Californian sea otters, *Enhydra*

lutris," by Thomas R. Loughlin, Jack A. Ames, and Judson E. Vandevere 347

ANTONELIS, GEORGE A., JR., STEPHEN LEATHERWOOD, and DANIEL K. ODELL, "Population growth and censuses of the northern elephant seal, *Mirounga angustirostris*, on the California Channel Islands, 1958-78" 562

Arabian gulf
fishes, food
proximate composition and nutritive value 211

ARMSTRONG, DAVID A.—see STEVENS and ARMSTRONG

ARNOLD, C. R.—see HOLT et al.

"Assimilation efficiency and nitrogen excretion of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae)," by Edward G. Durbin and Ann G. Durbin 601

Atherinops affinis—see Topsmelt

Atlantic, northwest
food of 10 species of juvenile groundfish 200

Atlantic, western
crab, xanthid
Micropanope sculptipes, complete larval development in laboratory 487

Atlantic, western North
billfishes
analysis of catch and effort data from U.S. recreational fishery, 1971-78 49
hagfishes
description of two new species 69

Atlantic Bight, Middle
diel-depth distribution of summer ichthyoplankton .. 705

Atlantic coast
alewife
offshore distribution 473
herring, blueback
offshore distribution 473

Australia
tuna, skipjack
distribution and life history 85

BARKER, SETH L., DAVID W. TOWNSEND, and JOHN S. HACUNDA, "Mortalities of Atlantic herring, *Clupea h. harengus*, smooth flounder, *Liopsetta putnami*, and rainbow smelt, *Osmerus mordax*, larvae exposed to acute thermal shock" 198

BEACH, RICHARD J.—see AINLEY et al.

BEARDLSEY, GRANT L., and RAMON J. CONSER, "An analysis of catch and effort data from the U.S. recreational fishery for billfishes (Istiophoridae) in the western North Atlantic Ocean and Gulf of Mexico, 1971-78" 49

Bering Sea, eastern
new fishes 353

Billfishes
U.S. recreational fishery, 1971-78
catch model 59
data acquisition 52
fishing techniques 50
longline fishery 50
marlin, blue 60, 64
marlin, white 60, 64
methodology 53
sailfish 61, 65
sampling coverage 53
sampling problems 52
sampling program 51

BIRD, PATRICIA M., "The occurrence of *Cirolana borealis* (Isopoda) in the hearts of sharks from Atlantic coastal waters of Florida" 376

Bivalves
deep-burrowing infaunal
flushing-coring device for collecting in intertidal sand 383

BLACKBURN, MAURICE, and D. L. SERVENTY, "Observations on distribution and life history of skipjack tuna, *Katsuwonus pelamis*, in Australian waters" 85

BOEHLERT, GEORGE W., "The effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diploproa* and a comparison with growth in the field" 789

BOWMAN, RAY E., "Food of 10 species of northwest Atlantic juvenile groundfish" 200

BREGE, DEAN A., "Growth characteristics of young-of-the-year walleye, *Stizostedion vitreum vitreum*, in John Day Reservoir on the Columbia River, 1979" 567

Brevoortia patronus—see Menhaden, Gulf

Brevoortia tyrannus—see Menhaden, Atlantic

"Burst swimming performance of northern anchovy, *Engraulis mordax*, larvae," by P. W. Webb and R. T. Corolla 143

California
sea otters
annual reproduction, dependency period, and apparent gestation period 347

California, central
rockfish, olive
growth, reproduction, and food habits 533

California, southern
fishes
crepuscular and nocturnal activites 1

California Bight, Southern
anchovy, northern
feeding selectivity of schools 131

California Channel Islands
seal, northern elephant
population growth and censuses, 1958-78 562

Callinectes bocourti—see Crab, tropical swimming

Callorhinus ursinus—see Seal, northern fur

Cancer magister—see Crab, Dungeness

Carcharhinus plumbeus—see Shark, sandbar

CAREY, FRANCIS G., and BRUCE H. ROBISON, "Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry" 277

"Carolinian records for American lobster, *Homarus americanus*, and tropical swimming crab, *Callinectes bocourti*. Postulated means of dispersal," by Austin B. Williams and David McN. Williams 192

CARRANZA, FRANCISCO—see STEVENSON and CARRANZA

"Cephalopods in the diet of the swordfish, *Xiphias gladius*, from the Florida Straits," by Ronald B. Toll and Steven C. Hess 765

CHANEY, ED—see WAHLE and CHANEY

Cheilotrema saturnum—see Croaker, black

CHESS, JAMES R.—see HOBSON et al.

Chinocoteague Bay, Virginia
shark, sandbar
feeding behavior and biology 441

Chionoecetes bairdi—see Crab, snow

CHITTENDEN, MARK E., JR.—see SHLOSSMAN and CHITTENDEN

Cirolana borealis
occurrence in shark hearts, Atlantic coastal waters of Florida
histopathology of shark heart 379
isopods in shark samples 379
sampling 378
shark pathology 379
water parameters 378

Citharichthys stigmaeus—see Sanddab, speckled

"Cleaning symbiosis between topsmelt, *Atherinops affinis*, and gray whale, *Eschrichtius robustus*, in Laguna San Ignacio, Baja California Sur, Mexico," by Steven L. Swartz 360

Clupea harengus harengus—see Herring, Atlantic

Cod, Atlantic
food of juvenile 202
Gulf of Maine
trophic relationships 775

COHEN, DANIEL M.—see YABE et al.

Columbia River
John Day Reservoir
walleye, growth characteristics of young-of-the-year, 1979 567
Wind River drainage
salmon, chinook, establishment of nonindigenous runs, 1955-63 507

Columbia River, mid-
sturgeon, white
diel and seasonal movements 367

COMPAGNO, L. J. V.—see GRUBER and COMPAGNO

"(The) complete larval development in the laboratory of *Micropanope sculptipes* (Crustacea, Decapoda, Xanthidae) with a comparison of larval characters in western Atlantic xanthid genera," by Bryan L. Andryszak and Robert H. Gore 487

CONSER, RAMON J.—see BEARDSLEY and CONSER

"Contribution to the life history of the deep-sea king crab, *Lithodes couesi*, in the Gulf of Alaska," by David A. Somerton 259

COROLLA, R. T.—see WEBB and COROLLA

"(A) correlation between annual catches of Dungeness crab, *Cancer magister*, along the west coast of North America and mean annual sunspot number," by Milton S. Love and William V. Westphal 794

Costa Rica
Pacific thread herring fishery
maximum yield estimates 689

Crab, deep-sea king
life history, in Gulf of Alaska
adaptations for life on the upper slope 265
depth distribution 261
egg size 265
fecundity 263
female reproductive condition 262
parasites 265
sex ratio 261
size distribution 261
size of maturity 263

Crab, Dungeness
impairment of chemosensory antennular flicking response by petroleum hydrocarbons
animal collection and maintenance 641
apparatus, experimental 642
hydrocarbon concentrations 643
impairment and recovery of chemosensory detection 643
procedures 642
solutions, experimental 642

statistical analysis 643
mass mortality of female on southern Washington coast 349
North America, west coast
correlation between annual catches and mean annual sunspot number 794

Crab, snow
description of stage II zoeae from plankton of lower Cook Inlet, Alaska
comparison of North Pacific zoeae of the subfamily Oregoniinae 180
key for distinguishing stage II zoeae 181

Crab, tropical swimming
Carolinian records for, postulated means of dispersal 192

"Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of their scotopic visual pigments and the photic environment," by Edmund S. Hobson, William N. McFarland, and James R. Chess 1

Croaker, black
seasonal spawning cycle 561

"Current knowledge of larvae of sculpins (Pisces: Cottidae and allies) in northeast Pacific genera with notes on intergeneric relationships," by Sally L. Richardson 103

Cynoscion arenarius—see Seatrout, sand

"Daily patterns in the activities of the swordfish, *Xiphias gladius*, observed by acoustic telemetry," by Francis G. Carey and Bruce H. Robison 277

Damariscotta Lake, Maine
alewife, anadromous
difference in sex ratios between the top and bottom of a fishway 207

DEAN, J. M.—see RADTKE and DEAN

DeGRANGE, ANTHONY R.—see AINLEY et al.

Delaware
marine fisheries
alewives 585
bass, striped 588
clam, hard 587
clam, surf 583
crab, blue 583
croaker 587
dredges, clam 596
dredges, crab 596
dredges, oyster 595
eel, American 589
food finfishes 579
food shellfishes 580
industrial 579
lines 593
menhaden 581
mullet 588
nets, fyke 597
nets, gill 590
nets, pound 595
oceanographic regime 581
oyster, American 584
perch, white 589
pots 592
rakes 597
recreational 580
seines, haul 592
seines, purse 590
shad 586
spot 587
sturgeon 586
trawl, otter 593
weakfish 585

DeMARTINI, E. E., and ROBERT K. FOUNTAIN, "Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes" 547

"Description of stage II zoeae of snow crab, *Chionoecetes bairdii* (Oxyrhyncha, Majidae) from plankton of lower Cook Inlet, Alaska," by Evan Haynes 177

"Development of larvae and juveniles of the rockfishes *Sebastes entomelas* and *S. zacentrus* (family Scorpaenidae) and occurrence off Oregon, with notes on head spines of *S. mystinus*, *S. flavidus*, and *S. melanops*," by Wayne A. Laroche and Sally L. Richardson 231

"Diel and seasonal movements of white sturgeon, *Acipenser transmontanus*, in the mid-Columbia River," by James M. Haynes and Robert H. Gray 367

"Diel-depth distribution of summer ichthyoplankton in the Middle Atlantic Bight," by Arthur W. Kendall, Jr. and N. A. Naplin 705

"Difference in sex ratios of the anadromous alewife, *Alosa pseudoharengus*, between the top and bottom of a fishway at Damariscotta Lake, Maine," by David A. Libby 207

DIZON, ANDREW E.—see GOODING et al.; KAYA et al.

Dolphin, Atlantic bottlenose
movements and activities near Sarasota, Florida
data collection and analysis 672
food resources and feeding behavior 684
home range 675
reproduction and growth 685
social interactions 681
social structure 679
study area 672

Drum, red
effects of temperature and salinity on egg hatching and larval survival 569

DURBIN, ANN G.—see DURBIN and DURBIN

DURBIN, EDWARD G., and ANN G. DURBIN, "Assimilation efficiency and nitrogen excretion of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae)" 601

"Early zoeal stages of *Lebbeus polaris*, *Eualus suckleyi*, *E. fabricii*, *Spirontocaris arcuata*, *S. ochotensis*, and *Heptacarpus camtschaticus* (Crustacea, Decapoda, Caridea, Hippolytidae) and morphological characterization of zoeae of *Spirontocaris* and related genera," by Evan Haynes 421

"Economic feasibility of domestic groundfish harvest from western Alaska waters: a comparison of vessel types, fishing strategies, and processor locations," by C. M. Lynde 303

"(The) effect of the bottom on the fast start of flatfish *Citharichthys stigmaeus*," by P. W. Webb 271

"Effects of photoperiod and feeding on daily growth patterns in otoliths of juvenile *Tilapia nilotica*," by Kuniaki Tanaka, Yasuo Mugiya, and Juro Yamada 459

"(The) effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diploproa* and a comparison with growth in the field," by George W. Boehlert .. 789

"Effects of swimming path curvature on the energetics of fish motion," by Daniel Weihs 171

"Effects of temperature and salinity on egg hatching and larval survival of red drum, *Sciaenops ocellata*," by Joan Holt, Robert Godbout, and C. R. Arnold 569

Embassichthys bathybius—see Sole, deepsea

Engraulis mordax—see Anchovy, northern

Enhydra lutris—see Otter, sea

ENNIS, G. P., "Fecundity of the American lobster, *Homarus americanus*, in Newfoundland waters" 796

Eschrichtius robustus—see Whale, gray

"Establishment of nonindigenous runs of spring chinook salmon, *Oncorhynchus tshawytscha*, in the Wind River drainage of the Columbia River, 1955-63," by Roy J. Wahle and Ed Chaney 507

"Estimated growth of surface-schooling skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, from the Papua New Guinea region," by J. W. J. Wankowski 517

Eualus fabricii
description
stage I and II zoeae 430

Eualus suckleyi
decription
stage I zoeae 426
stage II zoeae 429

Eumetopias jubatus—see Sea lion, Steller

Euthynnus affinis—see Tuna

"Fecundity of the American lobster, *Homarus americanus*, in Newfoundland waters," by G. P. Ennis . 796

"Feeding behavior and biology of young sandbar sharks, *Carcharhinus plumbeus* (Pisces, Carcharhinidae), in Chincoteague Bay, Virginia," by Robert J. Medved and Joseph A. Marshall 441

"Feeding periodicity and diel variation in diet composition of subyearling coho salmon, *Oncorhynchus kisutch*, and steelhead, *Salmo gairdneri*, in a small stream during summer," by James H. Johnson and Emily Z. Johnson . 370

"Feeding rate of captive adult female northern fur seals, *Callorhinus ursinus*," by Stephen Spotte and Gary Adams 182

"Feeding selectivity of Dover sole, *Microstomus pacificus*, off Oregon," by Wendy L. Gabriel and William G. Pearcy 749

"Feeding selectivity of schools of northern anchovy, *Engraulis mordax*, in the Southern California Bight," by J. Anthony Koslow 131

FERNHOLM, BO, and CARL L. HUBBS, "Western Atlantic hagfishes of the genus *Eptatretus* (Myxinidae) with description of two new species" 69

Fish motion
effects of swimming path curvature on energetics ... 171

Fish schools
stochastic model for size of
fitting model to data 318
observations 316
sensitivity analysis 319

Fishes
new to eastern Bering Sea
Kali indica 353
Laemonema longipes 354
Macropinna microstoma 354
Percis japonicus 353

"Fishes new to the eastern Bering Sea," by Mamoru Yabe, Daniel M. Cohen, Kiyoshi Wakabayashi, and Tomio Iwamoto 353

Fishes, Californian nearshore
crepuscular and nocturnal activities
activity patterns 19
day and night feeders 18
day feeders 8
determining activity patterns in fishes 3
determining spectral composition of submarine sunlight 2
determining spectral photosensitivity of fishes 3
night feeders 15
scotopic spectral sensitivity and ambient light 23
scotopic spectral sensitivity and bioluminescence . 24
submarine daylight 3
submarine nightlight 5

Fishes, demersal
trophic relationships in Gulf of Maine
benthos analysis 783
dietary overlap 781
fish abundance 777
foods 777
prey size and predator mouth morphology 782

Fishes, food
Arabian Gulf
proximate composition and nutritive value 211

FLINT, R. WARREN, and NANCY N. RABALAIS, "Gulf of Mexico shrimp production: A food web hypothesis" .. 737

Florida
Atlantic coastal waters
occurrence of *Cirolana borealis* in shark hearts ... 376

Florida Straits
swordfish
cephalopods in the diet 765

Flounder, smooth
mortalities of larvae exposed to acute thermal shock 198

Flounder, winter
Gulf of Maine
trophic relationships 775

Flounder, yellowtail
food of juvenile 205
Gulf of Maine
trophic relationships 775

"(A) flushing-coring device for collecting deep-burrowing bivalves in intertidal sand," by Mark James Grussendorf 383

"Food of 10 species of northwest Atlantic juvenile groundfish," by Ray E. Bowman 200

FOUNTAIN, ROBERT K.—see DeMARTINI and FOUNTAIN

FROST, KATHRYN J., and LLOYD F. LOWRY, "Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationships" 187

FRY, BRIAN, "Natural stable carbon isotope tag traces Texas shrimp migrations" 337

GABRIEL, WENDY L., and WILLIAM G. PEARCY, "Feeding selectivity of Dover sole, *Microstomus pacificus*, off Oregon" 749

Gadids, marine
Alaska, northern
trophic importance of, and their body-otolith size relationships 187

Gadus morhua—see Cod, Atlantic

GEORGE, K. A.—see AL-JUDAIMI et al.

Gill nets
salmon
mortality of seabirds in high-seas 800

GODBOUT, ROBERT—see HOLT et al.

GOLDBERG, STEPHEN R., "Seasonal spawning cycle of the black croaker, *Cheilotrema saturnum* (Sciaenidae)" 561

GOODING, REGINALD M., WILLIAM H. NEILL, and ANDREW E. DIZON, "Respiration rates and low-oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*" 31

GORE, ROBERT H.—see ANDRYSZAK and GORE

GRAHAM, JOSEPH J.—see TOWNSEND and GRAHAM

GRAY, ROBERT H.—see HAYNES and GRAY

Groundfish
economic feasibility of domestic harvest from western Alaska waters
comparison of fishing strategies 309
comparison of vessel types 308
cost derivations and sources of estimates 313
delivering at sea versus delivering to port 307
economic model 304
fishing strategy 307
fuel price 307
processor location and mode of operation 306
sensitivity to changes in fuel price 309
vessel types 306
food of juvenile 200

"Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, off central California," by Milton S. Love and William V. Westphal 533

"Growth, and age structure of larval Atlantic herring, *Clupea harengus harengus*, in the Sheepscot River estuary, Maine, as determined by daily growth increments in otoliths," by David W. Townsend and Joseph J. Graham 123

"Growth characteristics of young-of-the-year walleye, *Stizostedion vitreum vitreum*, in John Day Reservoir on the Columbia River, 1979," by Dean A. Brege 567

Growth curves
method for comparisons 95

"Growth rates of North Pacific albacore, *Thunnus alalunga*, based on tag returns," by R. Michael Laurs and Jerry A. Weatherall 293

GRUBER, S. H., and L. J. V. COMPAGNO, "Taxonomic status and biology of the bigeye thresher, *Alopias superciliosus*" 617

GRUSSENDORF, MARK JAMES, "A flushing-coring device for collecting deep-burrowing infaunal bivalves in intertidal sand" 383

Gulf of Alaska
crab, deep-sea king
life history 259
sea lion, Steller
prey of 467

Gulf of California
schooling of scalloped hammerhead shark 356

Gulf of Maine
trophic relationships among demersal fishes 775

Gulf of Mexico
billfishes
analysis of catch and effort data from U.S. recreational fishery, 1971-78 49
shrimp production
food web hypothesis 737

"Gulf of Mexico shrimp production: A food web hypothesis," by R. Warren Flint and Nancy N. Rabalais 737

HACUNDA, JOHN S., "Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine" . 775

HACUNDA, JOHN S.—see BARKER et al.

Haddock
food of juvenile 203

Hagfishes
Atlantic, western
Eptatretus minor 78
Eptatretus multidens 80
Eptatretus species A and B 76
Eptatretus species C 77
Eptatretus springeri 74
generic allocation 72
species key 73

Hake, red
food of juvenile 204
Gulf of Maine
trophic relationships 775

Hake, silver
food of juvenile 203

Hake, spotted
food of juvenile 204

Hake, white
food of juvenile 204

HAYNES, EVAN, "Description of stage II zoeae of snow crab, *Chionoecetes bairdii* (Oxyrhyncha, Majidae) from plankton of lower Cook Inlet, Alaska" 177

HAYNES, EVAN, "Early zoeal stages of *Lebbeus polaris*, *Eualus suckleyi*, *E. fabricii*, *Spirontocaris arcuata*, *S. ochotensis*, and *Heptacarpus camtschaticus* (Crustacea, Decapoda, Caridea, Hippolytidae) and morphological characterization of zoeae of *Spirontocaris* and related genera" 421

HAYNES, JAMES M., and ROBERT H. GRAY, "Diel and seasonal movements of white sturgeon, *Acipenser transmontanus*, in the mid-Columbia River" 367

HENDRIX, SHARON D.—see KAYA et al.

Heptacarpus camtschaticus
description
stage I zoeae 434

Herring, Atlantic
mortalities of larvae exposed to acute thermal shock 198
Sheepscot River estuary, Maine
growth and age structure of larval, as determined by daily growth increments in otoliths 123

Herring, blueback
offshore distribution along the Atlantic coast
commercial catches 481
depth distribution 482
seasonal distribution 476

Herring, thread
maximum yield estimates for Costa Rica fishery
catch and effort statistics estimation 692
management implications 701
model evaluation 699
unit stock definition 691
yield analyses 694

HESS, STEVEN C.—see TOLL and HESS

Hippolytidae
early zoeal stages
characterization of zoeae of *Spirontocaris* s.s. and related genera 438
comparison of zoeal stages with descriptions by other authors 435
description 422

"Histochemical indications of liver glycogen in samples of emaciated and robust larvae of the northern anchovy, *Engraulis mordax*," by Charles P. O'Connell and Pedro A. Paloma 806

HOBSON, EDMUND S., WILLIAM N. McFARLAND, and JAMES R. CHESS, "Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of their scotopic visual pigments and the photic environment" 1

HOLT, JOAN, ROBERT GODBOUT, and C. R. ARNOLD, "Effects of temperature and salinity on egg hatching and larval survival of red drum, *Sciaenops ocellata*" 569

Homarus americanus—see Lobster, American

HUBBS, CARL L.—see FERNHOLM and HUBBS

HUNTER, J. ROE, and RODERICK LEONG, "The spawning energetics of female northern anchovy, *Engraulis mordax*" 215

Ichthyoplankton, summer
diel-depth distribution in Middle Atlantic Bight
Auxis sp. ... 723
Citharichthys arctifrons ... 717
Etropus microstomus ... 723
Hippoglossina oblonga ... 720
Merluccius bilinearis ... 712
Peprilus triacanthus ... 720
Pisodonophis cruentifer ... 721
Poronotus saltatrix ... 709
Urophycis spp. ... 720

"Impairment of the chemosensory antennular flicking response in the Dungeness crab, *Cancer magister*, by petroleum hydrocarbons," by Walter H. Pearson, Peter C. Sugarman, Dana L. Woodruff, and Bori L. Olla ... 641

"Induced spawning of a tuna, *Euthynnus affinis*," by Calvin M. Kaya, Andrew E. Dizon, and Sharon D. Hendrix ... 185

IRVINE, A. BLAIR, MICHAEL D. SCOTT, RANDALL S. WELLS, and JOHN H. KAUFMANN, "Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida" ... 671

Istiophorus platypterus—see Sailfish

IWAMOTO, TOMIO—see YABE et al.

JAFRI, A. K.—see AL-JUDAIMI et al.

JOHNSON, EMILY Z.—see JOHNSON and JOHNSON

JOHNSON, JAMES H., and EMILY Z. JOHNSON, "Feeding periodicity and diel variation in diet composition of subyearling coho salmon, *Oncorhynchus kisutch*, and steelhead, *Salmo gairdneri*, in a small stream during summer" ... 370

JONES, LINDA L.—see AINLEY et al.

KAPPENMAN, RUSSELL F., "A method for growth curve comparisons" ... 95

Katsuwonus pelamis—see Tuna, skipjack

KAUFMANN, JOHN H.—see IRVINE et al.

KAYA, CALVIN M., ANDREW E. DIZON, and SHARON D. HENDRIX, "Induced spawning of a tuna, *Euthynnus affinis*" ... 185

KENDALL, ARTHUR W., JR., and N. A. NAPLIN, "Diel-depth distribution of summer ichthyoplankton in the Middle Atlantic Bight" ... 705

KLIMLEY, A. PETER, and DONALD R. NELSON, "Schooling of the scalloped hammerhead shark, *Sphyrna lewini*, in the Gulf of California" ... 356

KOSLOW, J. ANTHONY, "Feeding selectivity of schools of northern anchovy, *Engraulis mordax*, in the Southern California Bight" ... 131

Laguna San Ignacio
Baja California Sur, Mexico
cleaning symbiosis between topsmelt and gray whale ... 360

LAROCHE, WAYNE A., and SALLY L. RICHARDSON, "Development of larvae and juveniles of the rockfishes *Sebastes entomelas* and *S. zacentrus* (family Scorpaenidae) and occurrence off Oregon, with notes on head spines of *S. mystinus*, *S. flavidus*, and *S. melanops*" ... 231

LAURS, R. MICHAEL, and JERRY A. WEATHERALL, "Growth rates of North Pacific albacore, *Thunnus alalunga*, based on tag returns" ... 293

LEATHERWOOD, STEPHEN—see ANTONELIS et al.

Lebbeus polaris
description
stage I zoeae ... 422
stage II zoeae ... 425

LEONG, RODERICK—see HUNTER and LEONG

LIBBY, DAVID A., "Difference in sex ratios of the anadromous alewife, *Alosa pseudoharengus*, between the top and bottom of a fishway at Damariscotta Lake, Maine" ... 207

Limanda ferruginea—see Flounder, yellowtail

Liopsetta putnami—see Flounder, smooth

Lithodes couesi—see Crab, deep-sea king

Lobster, American
Carolinian records for, postulated means of dispersal 192
fecundity in Newfoundland waters ... 796

LOUGHLIN, THOMAS R., JACK A. AMES, and JUDSON E. VANDEVERE, "Annual reproduction, dependency period, and apparent gestation period in two Californian sea otters, *Enhydra lutris*" ... 347

LOVE, MILTON S., and WILLIAM V. WESTPHAL, "A correlation between annual catches of Dungeness crab, *Cancer magister*, along the west coast of North America and mean annual sunspot number" ... 794

LOVE, MILTON S., and WILLIAM V. WESTPHAL, "Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, off central California" ... 533

LOWRY, LLOYD F.—see FROST and LOWRY

LYNDE, C. M., "Economic feasibility of domestic groundfish harvest from western Alaska waters: a comparison of vessel types, fishing strategies, and processor locations" ... 303

McCLEOD, GUY C.—see ROBINSON et al.

McFARLAND, WILLIAM N.—see HOBSON et al.

McHUGH, J. L., "Marine fisheries of Delaware" ... 575

Macrozoarces americanus—see Pout, ocean

"Marine fisheries of Delaware," by J. L. McHugh 575

Marine fisheries—see Delaware

MARSHALL, JOSEPH A.—see MEDVED and MARSHALL

"Mass mortality of female Dungeness crab, *Cancer magister*, on the southern Washington coast," by Bradley G. Stevens and David A. Armstrong 349

"Maximum yield estimates for the Pacific thread herring, *Opisthonema* spp., fishery in Costa Rica," by David K. Stevenson and Francisco Carranza 689

MEDVED, ROBERT J., and JOSEPH A. MARSHALL, "Feeding behavior and biology of young sandbar sharks, *Carcharhinus plumbeus* (Pisces, Carcharhinidae), in Chincoteague Bay, Virginia" 441

Menhaden, Atlantic
assimilation efficiency and nitrogen excretion 601

Menhaden, Gulf
recruitment and exploitation
area-specific and age-specific exploitation rates ... 333
mortality rate estimation from adult tag recoveries 329
movement and recruitment of juvenile tagged fish 326
tagging methodology 325

"(A) method for growth curve comparisons," by Russell F. Kappenman 95

Micropanope sculptipes
complete larval development in laboratory
comparative morphology with other xanthid larvae 499
first zoea 490
fourth zoea 494
megalopa 497
plesiomorphy and larval development 503
second zoea 492
status of *Micropanope* in Family Xanthidae 505
third zoea 494

Microstomus pacificus—see Sole, Dover

Mirounga angustirostris—see Seal, northern elephant

"Morphological features of the otoliths of the sailfish, *Istiophorus platypterus*, useful in age determination," by Richard L. Radtke and J. M. Dean 360

MORSE, M. PATRICIA—see ROBINSON et al.

"Mortalities of Atlantic herring, *Clupea h. harengus*, smooth flounder, *Liopsetta putnami*, and rainbow smelt, *Osmerus mordax*, larvae exposed to acute thermal shock," by Seth L. Barker, David W. Townsend, and John S. Hacunda 198

"Mortality of seabirds in high-seas salmon gill nets," by David G. Ainley, Anthony R. DeGange, Linda L. Jones, and Richard J. Beach 800

"Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida," by A. Blair Irvine, Michael D. Scott, Randall S. Wells, and John H. Kaufmann 671

MUGIYA, YASUO—see TANAKA et al.

Myoxocephalus octodecemspinosus—see Sculpin, longhorn

NAPLIN, N. A.—see KENDALL and NAPLIN

"Natural stable carbon isotope tag traces Texas shrimp migrations," by Brian Fry 337

NEILL, WILLIAM H.—see GOODING et al.

NELSON, DONALD R.—see KLIMLEY and NELSON

NEVES, RICHARD J., "Offshore distribution of alewife, *Alosa pseudoharengus*, and blueback herring, *Alosa aestivalis*, along the Atlantic coast" 473

Newfoundland
fecundity of American lobster in waters 796

North America, west coast
crab, Dungeness
correlation between annual catches and mean annual sunspot number 794

"Observations on distribution and life history of skipjack tuna, *Katsuwonus pelamis*, in Australian waters," by Maurice Blackburn and D. L. Serventy 85

"(The) occurrence of *Cirolana borealis* (Isopoda) in the hearts of sharks from Atlantic coastal waters of Florida," by Patricia M. Bird 376

O'CONNELL, CHARLES P., and PEDRO A. PALOMA, "Histochemical indications of liver glycogen in samples of emaciated and robust larvae of the northern anchovy, *Engraulis mordax*" 806

ODELL, DANIEL K.—see ANTONELIS et al.

"Offshore distribution of alewife, *Alosa pseudoharengus*, and blueback herring, *Alosa aestivalis*, along the Atlantic coast," by Richard J. Neves 473

OLLA, BORI L.—see PEARSON et al.

Oncorhynchus kisutch—see Salmon, coho

Oncorhynchus tshawytscha—see Salmon, chinook

Opisthonema spp.—see Herring, thread

Oregon
rockfish
development of larvae and juveniles off 231

sole, Dover
feeding selectivity 749

Osmerus mordax—see Smelt, rainbow

"(The) osteology and relationships of the anglerfish genus *Tetrabrachium* with comments on lophiiform classification," by Theodore W. Pietsch 387

Otoliths
  sailfish
    morphological features useful in age determination 360

Otter, sea
  annual reproduction, dependency period, and apparent gestation period in two Californian 347

"Ovarian cycling frequency and batch fecundity of the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes," by E. E. DeMartini and Robert K. Fountain 547

Pacific, northeast
  sculpin larvae
    current knowledge with notes on intergeneric relationships 103

PALOMA, PEDRO A.—see O'CONNELL and PALOMA

Papua New Guinea
  skipjack tuna
    estimated growth of surface-schooling 517
  yellowfin tuna
    estimated growth of surface-schooling 517

PEARCY, WILLIAM G.—see GABRIEL and PEARCY

PEARSON, WALTER H., PETER H. SUGARMAN, DANA L. WOODRUFF, and BORI L. OLLA, "Impairment of the chemosensory antennular flicking response in the Dungeness crab, *Cancer magister*, by petroleum hydrocarbons" 641

"Pelagic eggs and larvae of the deepsea sole, *Embassichthys bathybius* (Pisces: Pleuronectidae), with comments on generic affinities," by Sally L. Richardson ... 163

Penaeus aztecus—see Shrimp, brown

PIETSCH, THEODORE W., "The osteology and relationships of the anglerfish genus *Tetrabrachium* with comments on lophiiform classification" 387

PITCHER, KENNETH W., "Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska" 467

Placopecten magellanicus—see Scallop, deep-sea

Plaice, American
  food of juvenile 204

Pollock
  food of juvenile 203

"Population growth and censuses of the northern elephant seal, *Mirounga angustirostris*, on the California Channel Islands, 1958-78," by George A. Antonelis, Jr., Stephen Leatherwood, and Daniel K. Odell 562

Pout, ocean
  Gulf of Maine
    trophic relationships 775

"Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska," by Kenneth W. Pitcher 467

"Proximate composition and nutritive value of some important food fishes from the Arabian Gulf," by Manal M. Al-Judaimi, A. K. Jafri, and K. A. George 211

Pseudopleuronectes americanus—see Flounder, winter

Queenfish
  ovarian cycling frequency and batch fecundity
    analysis of fish and ovaries 548
    annual egg production 554
    batch fecundity 551
    body size and time of spawning 549
    egg production and fish body size 556
    egg size 555
    field sampling 547
    ovarian cycling 550
    production cycles, timing of reproduction, and egg size 557
    relative fecundity 554
    residual ova 554
    sex ratio 551
    size at sexual maturity 555
    spawning frequency and annual fecundity 557
    spawning season and gonad maturation 549
    temporal patterns of spawning 556

RABALAIS, NANCY N.—see FLINT and RABALAIS

RADTKE, RICHARD L., and J. M. DEAN, "Morphological features of the otoliths of the sailfish, *Istiophorus platypterus*, useful in age determination" 360

Raja erinacea—see Skate, little

"Recruitment and exploitation of Gulf menhaden, *Brevoortia patronus*," by Dean W. Ahrenholz 325

"Reproduction, movements, and population dynamics of the sand seatrout, *Cynoscion arenarius*," by Philip A. Shlossman and Mark E. Chittenden, Jr. 649

"Respiration rates and low-oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*," by Reginald M. Gooding, William H. Neill, and Andrew E. Dizon 31

"Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivore, *Amphiprion percula*," by P. W. Webb 727

RICHARDSON, SALLY L., "Current knowledge of larvae of sculpins (Pisces: Cottidae and allies) in northeast Pacific genera with notes on intergeneric relationships" 103

RICHARDSON, SALLY L., "Pelagic eggs and larvae of the deepsea sole, *Embassichthy bathybius* (Pisces: Pleuronectidae), with comments on generic affinities" . 163

RICHARDSON, SALLY L.—see LAROCHE and RICHARDSON

ROBINSON, WILLIAM E., WILLIAM E. WEHLING, M. PATRICIA MORSE, and GUY C. McLEOD, "Seasonal changes in soft-body component indices and energy reserves in the Atlantic deep-sea scallop, *Placopecten magellanicus*" 449

ROBISON, BRUCE H.—see CAREY and ROBISON

Rockfish, olive
growth, reproduction, and food habits, off central California
age and growth 535
age determination 534
food habits 535, 542
juveniles 541
length-weight relationshps 537
maturation and reproduction 534, 537

Rockfish, sharpchin
development of larvae and juveniles off Oregon
distinguishing features 247
fin development 249
general development 248
identification 244
literature 243
morphology 249
occurrence 253
pigmentation 251
scale formation 251
spination 249

Rockfish, splitnose
effects of photoperiod and temperature on laboratory growth of juvenile 789

Rockfish, widow
development of larvae and juveniles off Oregon
distinguishing features 235
fin development 238
general development 235
identification 233
literature 233
morphology 236
occurrence 242
pigmentation 240
scale formation 239
spination 239

Rockling, fourbeard
food of juvenile 204

Sagittae
daily growth increments indicate age and growth
skipjack tuna 151
yellowfin tuna 151

Sailfish
morphological features of otoliths useful in age determination 360

Salmo gairdneri—see Steelhead

Salmon, chinook
establishment of nonindigenous runs in Wind River drainage of Columbia River, 1955-63
adult trapping and hauling 510
catch contribution 513
hatchery operations 511
hatchery returns-juvenile releases 512
Shipperd Falls counts 512
Shipperd Falls fishway 509
spawning ground surveys 513
Wind River spring chinook salmon transfers 514

Salmon, coho
feeding periodicity and diel variation in diet composition in small stream during summer 370

Sampler, flushing-coring
collect deep-burrowing infaunal bivalves in intertidal sand 383

Sanddab, speckled
effect of bottom on fast start
fast-start performance 273
kinematics 272

Sarasota, Florida
dolphin, Atlantic bottlenose, movements and activities 671

Scallop, deep-sea
seasonal changes in soft-body component indices and energy reserves
biochemical analysis of tissues 451
body component indices 450, 452
dry weight and biochemical analyses 453
gametogenic cycle 451
histochemical localization of energy reserves 453
histological and histochemical monitoring 450
standard scallop 451

"Schooling of the scalloped hammerhead shark, *Sphyrna lewini*, in the Gulf of California," by A. Peter Klimley and Donald R. Nelson 356

Sciaenops ocellata—see Drum, red

Scopthalmus aquosus—see Windowpane

SCOTT, MICHAEL D.—see IRVINE et al.

Sculpin, longhorn
Gulf of Maine
trophic relationships 775

Sculpins
current knowledge of larvae in northeast Pacific
larval characters 105
larval groups 106
ungrouped genera 113

Sea lion, Steller
prey of, in the Gulf of Alaska 467

Seabirds
mortality in high-seas salmon gill nets
entanglement rates 804

overall mortality 804
species observed 802

Seal, northern elephant
population growth and censuses, on the California Channel Islands, 1958-78 562

Seal, northern fur
feeding rate of captive adult female 182

"Seasonal changes in soft-body component indices and energy reserves in the Atlantic deep-sea scallop, *Placopecten magellanicus*," by William E. Robinson, William E. Wehling, M. Patricia Morse, and Guy C. McLeod 449

"Seasonal spawning cycle of the black croaker, *Cheilotrema saturnum* (Sciaenidae)," by Stephen R. Goldberg 561

Seatrout, sand
reproduction, movements, and population dynamics
age determination using scales 660
growth and age determination by length frequency 658
maturation and spawning periodicity 650
maximum size, lifespan, and mortality 662
nurseries and later movements 657
spawning areas, early nurseries, and movements . 655
total weight-, girth-, and standard length-total length relations 664

Sebastes diploproa—see Rockfish, splitnose

Sebastes entomelas—see Rockfish, widow

Sebastes flavidus
head spine notes, off Oregon 254

Sebastes melanops
head spine notes, off Oregon 254

Sebastes mystinus
head spine notes, off Oregon 254

Sebastes serranoides—see Rockfish, olive

Sebastes zacentrus—see Rockfish, sharpchin

Seriphus politus—see Queenfish

SERVENTY, D. L.—see BLACKBURN and SERVENTY

Shark, sandbar
feeding behavior and biology of, in Chincoteague Bay, Virginia 441

Shark, scalloped hammerhead
schooling in Gulf of California 356

Shark, thresher—see Thresher, bigeye

Sharks
Atlantic coastal waters of Florida
occurrence of *Cirolana borealis* in hearts 376

Sheepscot River estuary, Maine
herring, Atlantic
growth and age structure of larval, as determined by daily growth increments in otoliths 123

SHLOSSMAN, PHILIP A., and MARK E. CHITTENDEN, JR., "Reproduction, movements, and population dynamics of the sand seatrout, *Cynoscion arenarius*" .. 649

Shrimp, brown
natural stable carbon isotope tag traces Texas migrations
bay migrations 344
bay shrimp 339
offshore migrations 343
offshore samples 341
seasonality 341, 342
size and bay brown shrimp $\delta^{13}C$ 339

Shrimp production
Gulf of Mexico
food web hypothesis 737

Skate, little
Gulf of Maine
trophic relationships 775

Smelt, rainbow
mortalities of larvae exposed to acute thermal shock 198

Sole, deepsea
pelagic eggs and larvae
comparison 166
description 164
identification 164
occurrence 166

Sole, Dover
feeding selectivity off Oregon
diet changes with predator length 753
feeding habits 752
prey abundance patterns 759

SOMERTON, DAVID A., "Contribution to the life history of the deep-sea king crab, *Lithodes couesi*, in the Gulf of Alaska" 259

"(The) spawning energetics of female northern anchovy, *Engraulis mordax*," by J. Roe Hunter and Roderick Leong 215

Sphyrna lewini—see Shark, scalloped hammerhead

Spirontocaris arcuata
description
stage I zoeae 431

Spirontocaris ochotensis
description
stage I zoeae 433

SPOTTE, STEPHEN, and GARY ADAMS, "Feeding rate of captive adult female northern fur seals, *Callorhinus ursinus*" 182

Steelhead
feeding periodicity and diel variation in diet composition in small stream during summer 370

STEVENS, BRADLEY G., and DAVID A. ARMSTRONG, "Mass mortality of female Dungeness crab, *Cancer magister*, on the southern Washington coast" .. 349

STEVENSON, DAVID K., and FRANCISCO CARRANZA, "Maximum yield estimates for the Pacific thread herring, *Opisthonema* spp., fishery in Costa Rica" 689

Stizostedion vitreum vitreum—see Walleye

"(A) stochastic model for the size of fish schools," by James Jay Anderson 315

STRUHSAKER, PAUL—see UCHIYAMA and STRUHSAKER

Sturgeon, white
diel and seasonal movements in mid-Columbia River 367

SUGARMAN, PETER C.—see PEARSON et al.

SWARTZ, STEVEN L., "Cleaning symbiosis between topsmelt, *Atherinops affinis*, and gray whale, *Eschrichtius robustus*, in Laguna San Ignacio, Baja California Sur, Mexico" 360

Swordfish
daily patterns in activities, observed by acoustic telemetry
buoyancy 290
horizontal movements 284
navigation 279
oxygen 289
receiving 279
temperature 279, 290
transmitters 278
vertical movements and light 287
Florida Straits
cephalopods in the diet 765

TANAKA, KUNIAKI, YASUO MUGIYA, and JURO YAMADA, "Effects of photoperiod and feeding on daily growth patterns in otoliths of juvenile *Tilapia nilotica*" 459

"Taxonomic status and biology of the bigeye thresher, *Alopias superciliosus*," by S. H. Gruber and L. J. V. Compagno 617

Tetrabrachium—see Anglerfish

Thresher, bigeye
taxonomic status and biology
abundance, distribution, and habitat 632
age and growth 630
characters, distinctive 619
color 624
commercial importance 636
denticles 627
dentition 625
food 635
notes, descriptive 623
parasitology 636
prey catching 635
reproduction 633
size 628
status of *Alopias profundus* 621
studies, experimental 635
vertebrae 624

Thunnus alalunga—see Albacore

Thunnus albacares—see Tuna, yellowfin

Tilapia nilotica
otoliths, effects of photoperiod and feeding on daily growth patterns of juvenile
correlation between number of otolith rings and age in days after hatching 462
experiments under 24-h photoperiod 460
feeding experiments 460
feeding time and formation of otolith rings 463
formation of otolith rings under 12L-12D photoperiod 462
formation of otolith rings under 18L-6D and 6L-18D photoperiods 463
measurement of daily rowth rhythm 460
otolith preparation for scanning electron microscopy 460

TOLL, RONALD B., and STEVEN C. HESS, "Cephalopods in the diet of the swordfish, *Xiphias gladius*, from the Florida Straits" 765

Topsmelt
Laguna San Ignacio, Baja California Sur, Mexico
cleaning symbiosis between, and gray whale 360

TOWNSEND, DAVID W., and JOSEPH J. GRAHAM, "Growth and age structure of larval Atlantic herring, *Clupea harengus harengus*, in the Sheepscot River estuary, Maine, as determined by daily growth increments in otoliths" 123

TOWNSEND, DAVID W.—see BARKER et al.

"Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationships," by Kathryn J. Frost and Lloyd F. Lowry 187

"Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine," by John S. Hacunda 775

Tursiops truncatus—see Dolphin, Atlantic bottlenose

Tuna
induced spawning 185

Tuna, shipjack
age and growth as indicated by daily growth increments of sagittae 151
distribution and life history in Australian waters
food 92
length 89
seasonal distribution 88
sexual condition 91
spatial distribution 86

weight 89
estimated growth of surface-schooling, from the Papua New Guinea region
estimated length-at-age 526
recruitment and exploited size range 521
stock movements 525
respiration rates and low-oxygen tolerance limits
activity-related metabolism 41
angular acceleration and excess body temperature 45
interrelation of metabolic rate, swimming speed, and body weight 43
low-oxygen resistance 45
low-oxygen tolerance 36, 39
oxygen consumption 35, 38
oxygen uptake experiments 32, 37
source and preexperimental treatment of fish 32
"standard" metabolism 41
terminology relevant to tuna metabolism 40

Tuna, yellowfin
age and growth as indicated by daily growth increments of sagittae 151
estimated growth of surface-schooling, from the Papua New Guinea region
estimated length-at-age 526
recruitment and exploited size range 521
stock movements 525

UCHIYAMA, JAMES H., and PAUL STRUHSAKER, "Age and growth of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, as indicated by daily growth increments of sagittae" 151

Urophycis chuss—see Hake, red

VANDEVERE, JUDSON E.—see LOUGHLIN et al.

WAHLE, ROY J., and ED CHANEY, "Establishment of nonindigenous runs of spring chinook salmon, *Oncorhynchus tshawytscha*, in the Wind River drainage of the Columbia River, 1955-63" 507

WAKABAYASHI, KIYOSHI—see YABE et al.

Walleye
young-of-the-year growth characteristics in John Day Reservoir on the Columbia River, 1979 567

WANKOWSKI, J. W. J., "Estimated growth of surface-schooling skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, from the Papua New Guinea region" 517

Washington
southern coast
mass mortality of female Dungeness crab 349

WEATHERALL, JERRY A.—see LAURS and WEATHERALL

WEBB, P. W., "Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivore, *Amphiprion percula*" 727

WEBB, P. W., "The effect of the bottom on the fast start of flatfish *Citharichthys stigmaeus*" 271

WEBB, P. W., and R. T. COROLLA, "Burst swimming performance of northern anchovy, *Engraulis mordax*, larvae" 143

WEIHS, DANIEL, "Effects of swimming path curvature on the energetics of fish motion" 171

WEHLING, WILLIAM E.—see ROBINSON et al.

WELLS, RANDALL S.—see IRVINE et al.

"Western Atlantic hagfishes of the genus *Eptatretus* (Myxinidae) with description of two new species," by Bo Fernholm and Carl L. Hubbs 69

WESTPHAL, WILLIAM V.—see LOVE and WESTPHAL

Whale, gray
Laguna San Ignacio, Baja California Sur, Mexico
cleaning symbiosis between, and topsmelt 360

WILLIAMS, AUSTIN B., and DAVID McN. WILLIAMS, "Carolinian records for American lobster, *Homarus americanus*, and tropical swimming crab, *Callinectes bocourti*. Postulated means of dispersal" 192

WILLIAMS, DAVID McN.—see WILLIAMS and WILLIAMS

Windowpane
Gulf of Maine
trophic relationships 775

WOODRUFF, DANA L.—see PEARSON et al.

Xiphias gladius—see Swordfish

YABE, MAMORU, DANIEL M. COHEN, KIYOSHI WAKABAYASHI, and TOMIO IWAMOTO, "Fishes new to the eastern Bering Sea" 353

YAMADA, JURO—see TANAKA et al.

ERRATA

Fishery Bulletin, Vol. 79, No. 4

Antonelis, George A., Jr., Stephen Leatherwood, and Daniel K. Odell, "Population growth and censuses of the northern elephant seal, *Mirounga angustirostris*, on the California Channel Islands, 1958-78," p. 562-567.

Page 565, right column, second paragraph, line 4, correct to read:

ues reached 0.305 then dropped to 0.121 for 1964-

INFORMATION FOR CONTRIBUTORS TO THE *FISHERY BULLETIN*

Manuscripts submitted to the *Fishery Bulletin* will reach print faster if they conform to the following instructions. These are not absolute requirements, of course, but desiderata.

CONTENT OF MANUSCRIPT

The **title page** should give only the title of the paper, the author's name, his affiliation, and mailing address, including ZIP code.

The **abstract** should not exceed one double-spaced page.

In the **text,** *Fishery Bulletin* style, for the most part, follows that of the *U.S. Government Printing Office Style Manual*. Fish names follow the style of the American Fisheries Society Special Publication No. 12, *A List of Common and Scientific Names of Fishes from the United States and Canada*, Fourth Edition, 1980.

Text footnotes should be typed separately from the text.

Figures and **tables,** with their legends and headings, should be self-explanatory, not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript.

Preferably **figures** should be reduced by photography to 5¾ inches (for single-column figures, allowing for 50% reduction in printing), or to 12 inches (for double-column figures). The maximum height, for either width, is 14 inches. Photographs should be printed on glossy paper.

Do not send original drawings to the Scientific Editor; if they, rather than the photographic reductions, are needed by the printer, the Scientific Publications Office will request them.

Each **table** should start on a separate page. Consistency in headings and format is desirable. Vertical rules should be avoided, as they make the tables more expensive to print. Footnotes in tables should be numbered sequentially in arabic numerals. To avoid confusion with powers, they should be placed to the *left* of numerals.

Acknowledgments, if included, are placed at the end of the text.

Literature is cited in the text as: Lynn and Reid (1968) or (Lynn and Reid 1968). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited." Only the author's surname and initials are required in the **literature cited.** The accuracy of the **literature cited** is the responsibility of the author. Abbreviations of names of periodicals and serials should conform to *Serial Sources for the BIOSIS Data Base*. (*Chemical Abstracts* also uses this sytem, which was developed by the American Standards Association.)

Common **abbreviations** and **symbols,** such as mm, m, g, ml, mg, °C (for Celsius), %, ‰ and so forth, should be used. Abbreviate units of measure only when used with numerals. Periods are only rarely used with abbreviations.

We prefer that **measurements** be given in metric units; other equivalent units may be given in parentheses.

FORM OF THE MANUSCRIPT

The original of the manuscript should be typed, double-spaced, on white bond paper. Please triple space above headings. We would rather receive good duplicated copies of manuscripts than carbon copies. The sequence of the material should be:

TITLE PAGE
ABSTRACT
TEXT
LITERATURE CITED
APPENDIX
TEXT FOOTNOTES
TABLES (Each table should be numbered with an arabic numeral and heading provided)
LIST OF FIGURES (Entire figure legends)
FIGURES (Each figure should be numbered with an arabic numeral; legends are desired)

ADDITIONAL INFORMATION

Send the ribbon copy and two duplicated or carbon copies of the manuscript to:

Dr. Carl J. Sindermann, Scientific Editor
Fishery Bulletin
Northeast Fisheries Center
Sandy Hook Laboratory
National Marine Fisheries Service, NOAA
Highlands, NJ 07732

Fifty **separates** will be supplied to an author free of charge and 100 supplied to his organization. No covers will be supplied.

Contents–continued

LOVE, MILTON S., and WILLIAM V. WESTPHAL. A correlation between annual catches of Dungeness crab, *Cancer magister*, along the west coast of North America and mean annual sunspot number 794
ENNIS, G. P. Fecundity of the American lobster, *Homarus americanus*, in Newfoundland waters 796
AINLEY, DAVID G., ANTHONY R. DeGANGE, LINDA L. JONES, and RICHARD J. BEACH. Mortality of seabirds in high-seas salmon gill nets 800
O'CONNELL, CHARLES P., and PEDRO A. PALOMA. Histochemical indications of liver glycogen in samples of emaciated and robust larvae of the northern anchovy, *Engraulis mordax* 806

INDEX, VOLUME 79 813

▪ GPO 796-086